

# Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment

Andrew J. Pershing, Charles H. Greene, Jack W. Jossi,  
Loretta O'Brien, Jon K. T. Brodziak, and Barbara A. Bailey

Pershing, A. J., Greene, C. H., Jossi, J. W., O'Brien, L., Brodziak, J. K. T., and Bailey, B. A. 2005. Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. — ICES Journal of Marine Science, 62: 1511–1523.

We used principal component analysis (PCA) to explore interannual changes in a time-series lasting more than 40 years of zooplankton abundance from NOAA's Continuous Plankton Recorder (CPR) survey. This analysis identified a complex of taxa, including *Centropages typicus*, *Oithona* spp., *Pseudocalanus* spp., and *Metridia lucens* that followed a common pattern of interdecadal variability characterized by a dramatic increase in these taxa around 1990, followed by a rapid decline in 2002. All of these taxa showed a large proportional increase in winter abundance between the 1980s and 1990s. These changes could be driven by increased primary productivity during winter, caused by a large-scale freshening of the Northwest Atlantic Shelf. In addition to the “community shift” mode, the analysis found a strong mode of interannual variability attributed to previously described changes in the abundance of late-stage *Calanus finmarchicus*. To explore the impact of these modes on higher trophic levels, we correlated the zooplankton modes with recruitment time-series from 12 fish stocks from the Gulf of Maine region. Several significant correlations were found, suggesting that the changes in the zooplankton modes may reflect broad changes in the Gulf of Maine ecosystem.

© 2005 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: *Calanus*, *Centropages*, climate, Continuous Plankton Recorder, copepods, euphausiids, fish recruitment, Gulf of Maine, *Metridia*, *Oithona*, *Pseudocalanus*, zooplankton.

Received 2 July 2004; accepted 25 April 2005.

A. J. Pershing and C. H. Greene: Ocean Resources and Ecosystems Program, Cornell University, Ithaca, NY 14853, USA. J. W. Jossi: Narragansett Laboratory, 28 Tarzwell Drive, Narragansett, RI 02882, USA. L. O'Brien and J. K. T. Brodziak: Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026, USA. B. A. Bailey: Department of Statistics, University of Illinois at Urbana Champaign, 725 S. Wright Street, Champaign IL 61820, USA. Correspondence to A. J. Pershing: tel: +1 607 255 5552; fax: +1 607 255 2106; e-mail: [ajp9@cornell.edu](mailto:ajp9@cornell.edu).

## Introduction

The recent renewal of the Magnuson–Stevens Fisheries Conservation Act mandates that US NOAA Fisheries begin to employ “ecosystem-based fishery management” for stocks under their jurisdiction. While arguments over the exact meaning of ecosystem-based management are ongoing (Brodziak and Link, 2002), the general intention is that the fisheries management process must begin to include the effects of environmental variability on stock recruitment, where environment includes physical processes and lower trophic-level dynamics. The ecosystem-based approach has even greater potential for aiding long-term stock rebuilding plans mandated by the Magnuson–Stevens Fisheries Conservation Act. By combining characterizations of

long-term variability in important environmental indicators with recruitment models, it may be possible to provide bounds on future recruitment.

A prerequisite of ecosystem-based fishery management is an understanding of how the ecosystem in question varies in time, the processes driving the variability, and the impact of variability on the resource in question. There has been considerable effort in both the Pacific and the Atlantic to link variability in fish stocks with major climate modes such as the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO).

The response of ecosystems to this forcing can be classified as interannual modes and longer period “regime shift” modes (Pershing *et al.*, 2004). Earlier work in the Gulf of Maine has identified an interannual mode of environmental

variability associated with the NAO (Conversi *et al.*, 2001; Greene and Pershing, 2001; MERCINA, 2001). In this region, the association between NAO and local weather appears weak. Instead, the NAO affects the Gulf of Maine through its influence on the circulation and water mass properties of the Labrador Current (Drinkwater *et al.*, 2003) and Gulf Stream (Taylor and Stephens, 1998; Rossby and Benway, 2000). One to two years following a negative NAO winter, the changes in the large-scale circulation bring a relatively cold-water mass called Labrador Subarctic Slope Water (LSSW) (Greene and Pershing, 2001) around the Tail of the Grand Banks, along the continental shelf break, and as far south as the Middle Atlantic Bight (MERCINA, 2001; Drinkwater *et al.*, 2003). LSSW is found at depths between 150 and 250 m, and it intrudes into the deep basins of the Scotian Shelf and Gulf of Maine, displacing the warmer, more saline Atlantic Temperate Slope Water (ATSW). The slope water transitions occur over a broad region and are the strongest signal of the NAO mode; thus, this region is often referred to as the “Coupled Slope Water System” (CSWS) (MERCINA, 2001). The one- to two-year lag in the CSWS’s response to the NAO offers the potential for NAO-based forecasts of environmental conditions in the Gulf of Maine (Greene and Pershing, 2003).

Physical changes in the CSWS associated with the NAO appear to influence the abundance of *Calanus finmarchicus* in the Gulf of Maine (Greene and Pershing, 2001; MERCINA, 2001, 2004). Following positive NAO conditions, when ATSW is predominant in the CSWS, *C. finmarchicus* is generally more abundant, while the presence of LSSW is associated with reduced abundance. Although variability in *C. finmarchicus* has yet to be linked with fish recruitment, it does explain some of the variability in the number of right whale births (Greene *et al.*, 2003; Greene and Pershing, 2004).

The lag in the CSWS’s response to the NAO offers the potential for NAO-based forecasts of environmental conditions in the Gulf of Maine. However, it is unreasonable to expect that the CSWS is the only mode of interannual variability in the Gulf of Maine, and it is unlikely that any new modes will support interannual forecasts. Knowledge of long-term variability can still inform management decisions even in these cases. In ecosystems exhibiting regime shifts, defined as abrupt changes in the mean state of an ecosystem (deYoung *et al.*, 2004), the properties of the system remain relatively stable for several years. The regime shifts exhibited by zooplankton and fish populations in the north-eastern Pacific associated with the Pacific Decadal Oscillation are archetypal of this kind of dynamics (Francis *et al.*, 1998; Hare and Mantua, 2000; Mantua and Hare, 2002), although it now appears that the North Sea exhibits regime-shift dynamics (Beaugrand *et al.*, 2003; Beaugrand, 2004). Although the shift between regimes in these regions cannot be predicted at this time, simply knowing the current state provides valuable information.

Previous studies on ecosystem variability in the Gulf of Maine have focused almost exclusively on the large copepod, *Calanus finmarchicus*. Although *C. finmarchicus* dominates the springtime biomass in the Gulf of Maine, from the larval fish’s point of view, it is just one species out of a range of possible prey. *C. finmarchicus* is also unusual in that, owing to its preference for deep water during its over-wintering phase, shelf populations require consistent input of animals from deep-water stocks (Greene and Pershing, 2001). As a consequence, interannual variability in *C. finmarchicus* may be more indicative of changes in regional circulation than in local processes (Heath *et al.*, 1999). Thus, developing a better understanding of the interannual variability of other zooplankton taxa is essential for identifying changes in the Gulf of Maine.

## Methods

The main goal of our study is to document changes in the Gulf of Maine zooplankton community over the last four decades. This includes documenting relationships among various zooplankton taxa and between zooplankton and fish recruitment. This study is a natural extension of our earlier analysis of *C. finmarchicus* variability measured by the Gulf of Maine Continuous Plankton Recorder (CPR) survey (MERCINA, 2001, 2003).

The Gulf of Maine CPR programme, operated by NOAA Fisheries according to standard CPR protocols (Warner and Hays, 1994), began in 1961 and consists of a single transect between Boston, Massachusetts, and Cape Sable, Nova Scotia (Jossi and Goulet, 1993). The CPR filters zooplankton onto a silk gauze with a 270- $\mu\text{m}$  mesh size. As the instrument moves through the water, the gauze is advanced, providing a spatial record of the samples. The CPR is towed from a ship-of-opportunity at a depth of  $\sim 10$  m with approximately one transect occurring each month. After each cruise, the sample mesh is cut in sections representing 10 nautical miles and sent to the Plankton Sorting Center in Szczecin, Poland. The resulting data set consists of spatially indexed abundance of several zooplankton taxa and large phytoplankton species. For this paper, we concentrated on the zooplankton cycles in the centre of the Gulf of Maine, and excluded CPR samples from Cape Cod Bay (west of 70°W) and the Scotian Shelf (east of 66°W).

The CPR’s 270- $\mu\text{m}$  mesh means that it will undersample many of the small taxa, while the small aperture should result in undersampling of the larger taxa through avoidance (Clark *et al.*, 2001). Furthermore, since the CPR is towed horizontally, it does not provide a measure of total biomass, especially for species that migrate vertically. These factors make it difficult to compare absolute abundances between taxa; however, the consistency of the CPR record should make it possible to resolve changes within taxa and allow us to compare relative patterns.

### Creating the time-series

For our study, we selected seven of the most commonly occurring taxonomic groups in the CPR database: *Calanus finmarchicus* CV-VI, *Calanus* spp. CI-IV (primarily *C. finmarchicus* – J.W. Jossi, pers. obs.), *Centropages typicus* CIV-VI, *Oithona* spp. CIV-VI, *Pseudocalanus* spp. CVI, *Metridia lucens* CV-VI, and euphausiids. For each taxon, we computed its climatological seasonal cycle by fitting a periodic spline to the log-transformed abundance data. The spline function indicates the expected abundance on any day of the year. Then we subtracted the expected abundance for that date from the measured abundance, based on the seasonal cycle, creating a data set of anomalies from the seasonal cycle. The anomalies were then averaged over each year to produce a time-series of annual abundance anomalies. This procedure minimizes the impact of years when sampling was biased towards one portion of the year.

To examine relationships among the data, we performed a principal component analysis (PCA) on the zooplankton time-series (Wilks, 1995). The first few principal components provide a low dimensional approximation to the original data set and help identify common patterns underlying the data.

### Fish recruitment data

Using data from NMFS fisheries surveys (Azarovitz, 1981), we computed a measure of standardized recruitment for 12 stocks from the Gulf of Maine region. These stocks include cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*) from Georges Bank; cod, redfish (*Sebastes fasciatus*), winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoide*), witch flounder (*Glyptocephalus cynoglossus*), and yellowtail flounder from the Gulf of Maine; and yellowtail flounder, winter flounder, and summer flounder (*Paralichthys dentatus*) from southern New England (Northeast Fisheries Science Center, 2002). The standardized recruitment values were computed according to the formula:

$$R_s = \frac{(R/S)_{\text{obs}} - (R/S)_{\text{VPA}}}{\sigma}$$

where R and S are the recruitment and spawning-stock biomass, inferred from the observations (subscript obs) and the virtual population assessment (subscript VPA), respectively, and  $\sigma$  is the standard deviation of the observed-VPA series. The  $R_s$  procedure attempts to remove the portion of recruitment attributable to factors internal to the population (represented by the VPA and the spawning biomass), and should emphasize external forcing. The series were then normalized over the period 1980–2001 by subtracting the mean and dividing by the standard deviation.

Each recruitment time-series was compared with the leading modes from the zooplankton PCA by computing

the standard linear correlation and Spearman rank correlations. Fish recruitment series are often characterized by many years of low recruitment punctuated by a few years of very good recruitment. For data sets of this kind, the rank correlation is a more appropriate technique (Snedecor and Cochran, 1989).

## Results

The yearly abundance anomaly time-series provides the simplest measures of year-to-year changes in the zooplankton population in the Gulf of Maine (Figure 1). With the exception of the euphausiids, all of the taxa exhibit abundance changes close to or exceeding one order of magnitude, with the largest interannual variability being exhibited by *Centropages typicus* and *Oithona* spp. (Figure 1b, c). The most striking pattern in the time-series, one followed by the majority of copepods, is an abrupt shift to high abundance values in the 1990s after a period of low values. To simplify the narrative below, we will drop species names or “spp.” for all taxa for which this is unambiguous.

The gap in the CPR record in the mid-1970s and the “community shift” between 1989 and 1990 divide the time-series into three periods: an early period (1961–1974), a middle period (1978–1989), and a late period (1990–2003). The early period was characterized by low values for most taxa in most years. Generally, *C. finmarchicus* had average values with the exception of very low years in 1962, 1963, and 1970 (Figure 1a). At the start of the time-series, both *Centropages* (Figure 1b) and *Oithona* (Figure 1c) were relatively abundant, and reached a maximum in 1963. Between 1963 and 1964, both taxa declined. *Centropages* began to increase gradually from 1967 to the end of the early period, while *Oithona* remained low. During this period, *Pseudocalanus* followed a similar pattern with a maximum in 1963 and a gradual decrease through 1966 (Figure 1d). *Metridia* (Figure 1e) was relatively stable during this period, but it did reach a minimum in 1964 in concert with *Centropages* and *Oithona*. *Calanus* copepodites (Figure 1f) showed a steady decline throughout this period. Relative to the other taxa, euphausiid abundance was steady (Figure 1g); however, it was slightly lower during 1965–1966 and 1973–1974.

During the middle period between 1978 and 1989, *C. finmarchicus* increased steadily, reaching a maximum in 1987. Over this period, the association between *Centropages* and *Oithona* became more apparent. Both taxa had maxima in 1979, and both exhibited a gradual decline through 1987. A correspondence between *Pseudocalanus* and *Centropages* and *Oithona* became more apparent during the 1980s. Like the previous two taxa, *Pseudocalanus* had a local maximum in 1979 followed by generally low levels, with the exception of 1983. *Metridia* exhibited its maximum variability during this period and seemed to follow the *Centropages*–*Oithona* pattern. An interesting exception is an abrupt drop in abundance between 1983 and 1984.

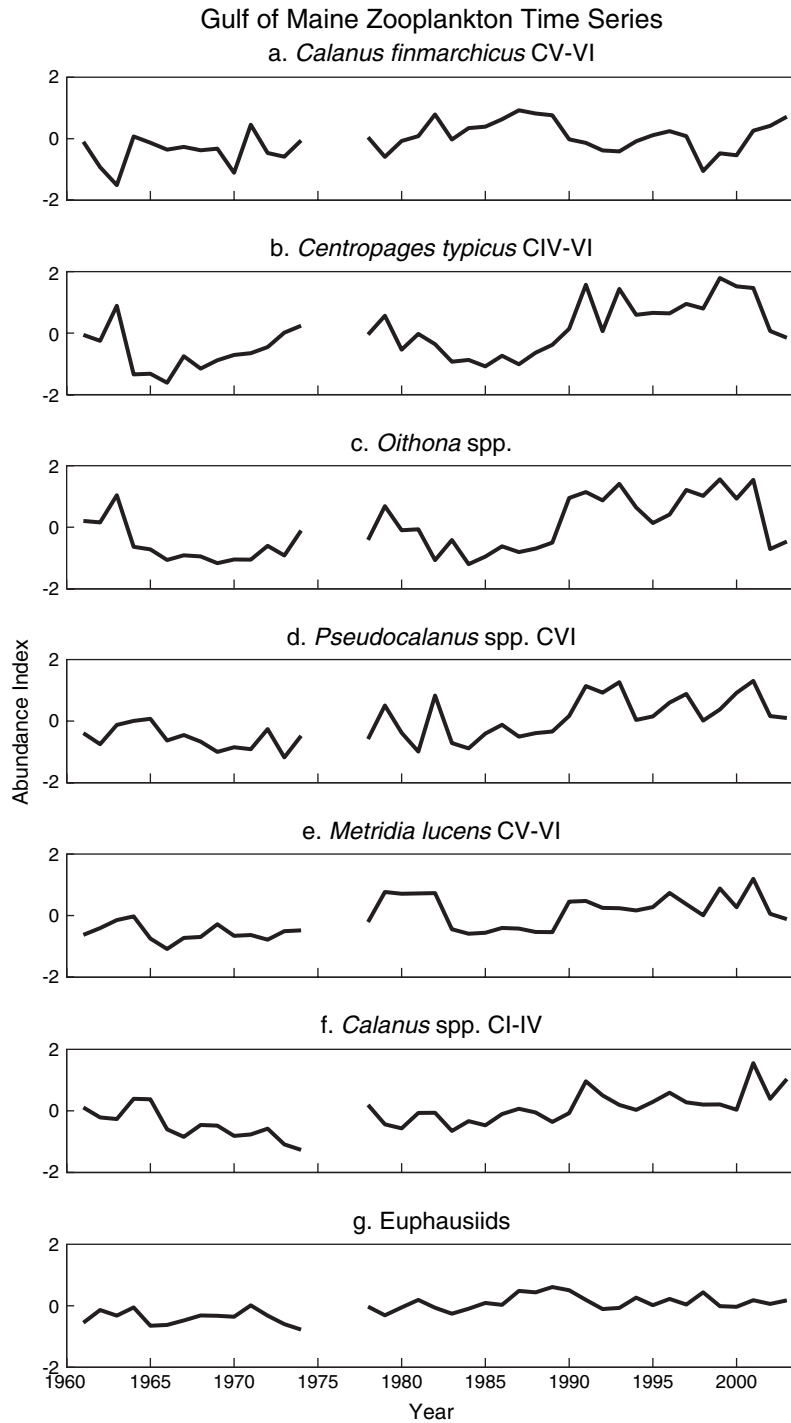


Figure 1. Time-series of annual mean abundance anomalies for seven taxa collected by the CPR. Each point in the time-series is the mean deviation between the observed log-transformed abundance values and the expected values based on the climatological seasonal cycle for that species, averaged over an entire year.

*Calanus* copepodites varied little during this period, but did show a slight increase between 1986 and 1988, the same period when *C. finmarchicus* reached its maximum. Like *C. finmarchicus*, euphausiids tended to increase through this period and reached their highest levels in the late 1980s.

Between 1989 and 1991, the Gulf of Maine zooplankton community went through a remarkable transition. During this brief period, *Centropages*, *Oithona*, *Pseudocalanus*, *Metridia*, and *Calanus* copepodites experienced a sudden increase in abundance. These taxa showed elevated abundance through the 1990s and then declined dramatically between 2001 and 2002, and except for *Calanus* copepodites, remained low in 2003. *C. finmarchicus* and euphausiid abundance patterns ran counter to the majority of the taxa. Both *C. finmarchicus* and euphausiids declined between 1989 and 1991 and remained low throughout the 1990s, relative to the late 1980s. In addition, *C. finmarchicus* experienced a dramatic decline in 1998 to levels not

seen since the 1960s. Earlier studies have attributed this decline to the changes in the hydrography and circulation of the northwestern Atlantic following the 1996 drop in the NAO (MERCINA, 2001, 2004; Pershing *et al.*, 2004).

### Statistical analysis

The most obvious pattern in the time-series is the dramatic shifts in abundance that occur on an approximately decadal scale. This pattern is present in the majority of taxa, with the notable exception of *C. finmarchicus*. Principal component analysis provides an objective way to quantify such associations. The first principal component, also called the leading mode, explains 64.7% of the total variation in the Gulf of Maine zooplankton community. This mode assigns large positive weights to *Centropages* and *Oithona*, moderate positive weights to *Pseudocalanus*, *Metridia*, and *Calanus* copepodites, and weak weights to *C. finmarchicus* (negative) and euphausiids (positive) (Figure 2a). When viewed as

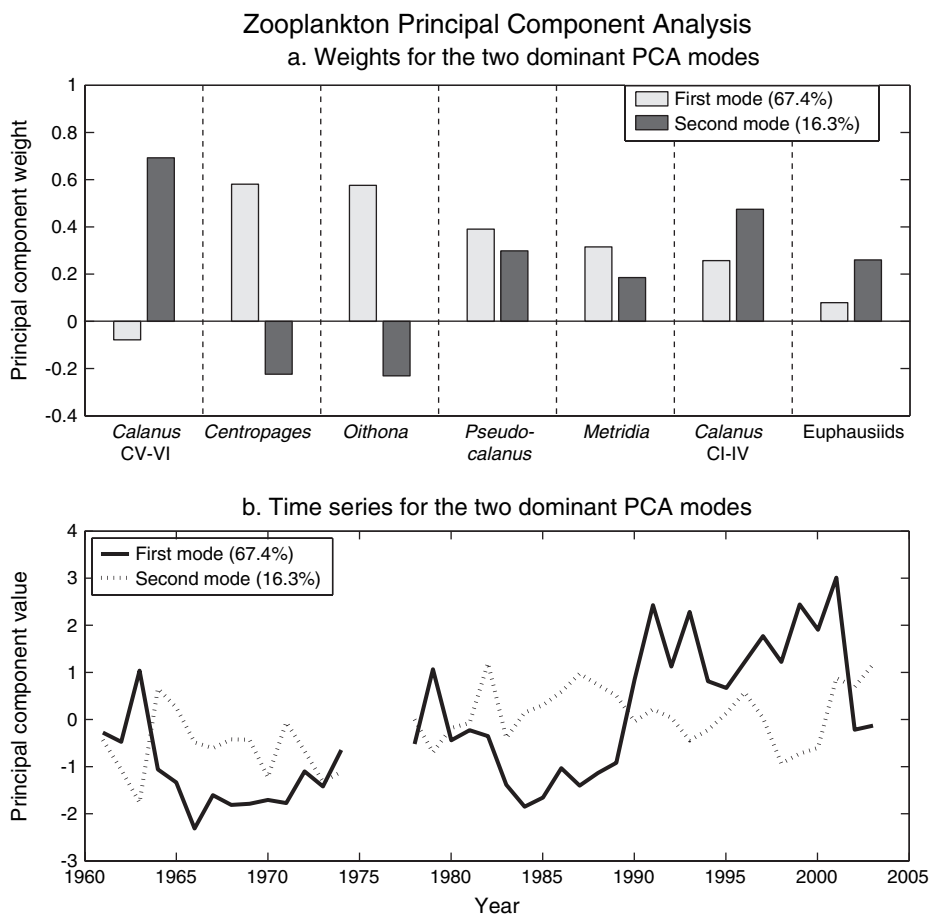


Figure 2. Summary of the principal component analysis (PCA) of the zooplankton time-series. (a) The principal component weights assigned to each taxa by the first mode (light grey) and the second mode (dark grey) from the PCA. (b) Principal component time-series for the two leading modes. These series are produced by multiplying the individual zooplankton time-series in Figure 1 by the appropriate weight from Figure 2a, and adding the series together.

a time-series (Figure 2b), the leading mode captures the community transitions exemplified by *Centropages* and *Oithona*. The second principal component accounts for 16.3% of the total variance. This mode assigns a strong positive weight to *C. finmarchicus*, moderate positive weights to *Calanus* copepodites, *Pseudocalanus*, *Metridia*, and euphausiids, and moderate negative weights to *Centropages* and *Oithona* (Figure 2a). The time-series corresponding to this mode is very similar to that for *C. finmarchicus* (Figure 2b). Together, these two modes capture 84% of the total variance in the zooplankton data set.

The PCA identified groups of taxa with similar year-to-year patterns. As implied by the PCA, *Centropages*, *Oithona*, *Pseudocalanus*, *Metridia*, and *Calanus* copepodites are all significantly correlated with one another (Table 1). The correlation is strongest between *Centropages* and *Oithona* ( $r^2 = 0.78$ ;  $p < 0.01$ ). *C. finmarchicus* is negatively correlated with both *Centropages* and *Oithona*, although only the *Oithona* correlation is significant ( $r^2 = 0.12$ ,  $p < 0.05$ ). *C. finmarchicus* exhibits a significant positive correlation with euphausiids ( $r^2 = 0.22$ ,  $p < 0.01$ ) and a weaker, non-significant correlation with *Calanus* copepodites.

### Community shift: a closer look

The most striking pattern in the Gulf of Maine time-series is the abrupt shift in the relative abundance of the major copepods that occurred around 1989. To better understand the nature of the 1989 community shift, we need to take a closer look at the seasonal cycles of the taxa and how they differ between the 1980s and the 1990s.

The seven zooplankton taxa have very different climatological annual cycles, reflecting the diversity of life history strategies in this community (Figure 3, heavy black lines). *C. finmarchicus* is abundant throughout the year and peaks in late spring (Figure 3a). In the Gulf of Maine, *Centropages* has a strong seasonal cycle reaching maximum abundance in late summer and minimum abundance in spring (Figure 3b). For both *C. finmarchicus* and *Centropages*, the seasonal cycles from the CPR are similar to those computed using net surveys (Meise and O'Reilly, 1996; Kane, 1999). *Oithona* is common from late spring through early winter, but has a noticeable dip in abundance in late winter (Figure 3c).

*Pseudocalanus*, like *C. finmarchicus*, is most abundant in late spring and early summer, following the spring bloom. *Pseudocalanus* has a smaller abundance peak in the autumn. *Metridia* is most abundant in autumn and winter (Figure 3e). *Calanus* copepodites have the most prominent seasonal cycle of any taxa (Figure 3f). Their abundance increases rapidly at the beginning of the year, and peaks at the beginning of spring, 32 days before *C. finmarchicus* reaches its peak abundance. Following its spring peak, *Calanus* copepodite abundance declines steadily throughout the year, although there are small peaks around days 190 and 270. Euphausiids vary little over the course of the year, but their abundance is slightly higher in spring and from late summer through autumn.

To more closely examine the differences between the early, middle, and late time periods, spline functions were fit to each taxon's data from the three periods. Concerning the 1989 shift, the most interesting comparisons are between the cycles for middle period (Figure 3, dashed lines) and the late period (Figure 3, light, solid lines). Early in the year, both the middle and late period cycles for *C. finmarchicus* closely resemble the climatological cycle (Figure 3a). Differences begin to appear near the spring abundance peak. Both the middle and late cycles had larger peaks than the climatological cycle, but the late period peak is slightly smaller and occurs before that from the middle period. The biggest difference occurs during autumn. During this season, both cycles show a slight peak, but the middle period peak is much larger, indicating nearly an order of magnitude decrease in the *C. finmarchicus* population between the 1980s and 1990s. Prior to the 1989 shift, *Centropages* was nearly absent from the Gulf of Maine during the first half of the year, a pattern also reflected in MARMAP net surveys (Kane, 1999). During the 1990s, *Centropages* increased throughout the year. Like *Centropages*, *Oithona* and *Pseudocalanus* were higher throughout the year in the 1990s compared with the 1980s. Other than a brief period in early spring, *Metridia* abundance in the 1990s was higher than they were in the 1980s throughout the year. In the 1990s, *Calanus* copepodites were more abundant during much of the year than they were in the 1980s, especially during winter. Euphausiid abundance increased during summer in the 1990s, but was lower during the rest of the year.

Table 1. Pairwise correlations between the zooplankton taxa expressed as  $r^2$ . Correlations significant at 95% and 99% level are indicated by \* and \*\*, respectively.

Taxon	<i>Centropages</i>	<i>Oithona</i>	<i>Pseudocalanus</i>	<i>Metridia</i>	<i>Calanus</i> CI-IV	Euphausiids
<i>C. finmarchicus</i> CV-CVI	0.07	0.12*	0.00	0.00	0.06	0.22**
<i>Centropages typicus</i>		0.78**	0.46**	0.49**	0.21**	0.06
<i>Oithona</i> spp.			0.51**	0.47**	0.27**	0.07
<i>Pseudocalanus</i> spp.				0.45**	0.49**	0.08
<i>Metridia lucens</i>					0.31**	0.17**
<i>Calanus</i> CI-CIV						0.24**

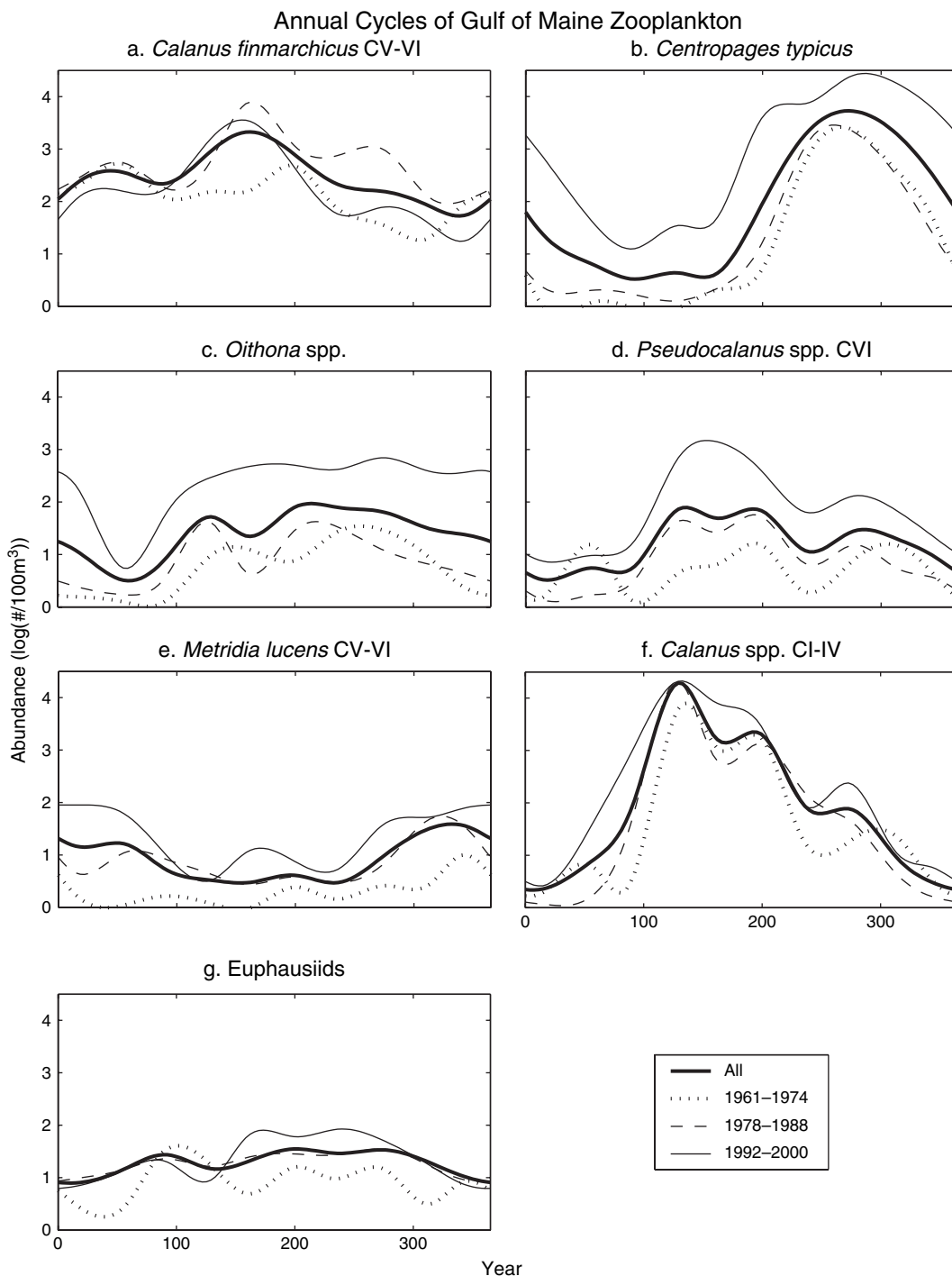


Figure 3. Annual cycles of abundance for the seven zooplankton time-series. For each taxon, a periodic spline was fit to the entire data set (heavy line) and to data from three periods: 1961–1974 (dotted), 1978–1988 (dashed), and 1992–2000 (solid).

For a population that is growing rapidly, a small change in abundance can result in very large changes weeks or months later. Thus, large differences among the seasonal cycles in the 1980s and 1990s typically occur near the

abundance peaks and do not necessarily reflect the time of greatest change. One way to reduce the growth effect is to look at the change expressed as a proportion of the prior period, e.g. the change in abundance between the 1980s

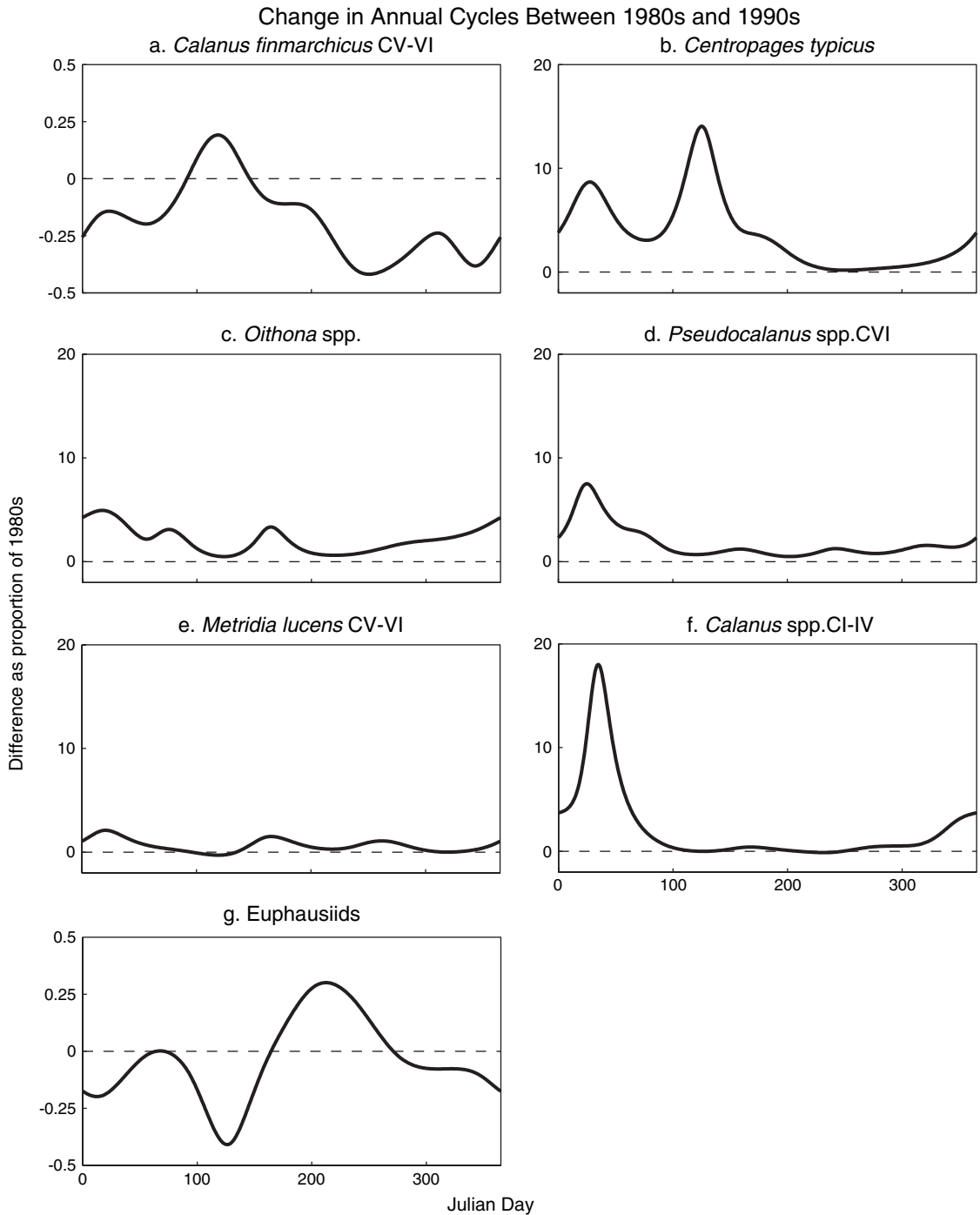


Figure 4. Change in the annual cycles between the 1980s and 1990s expressed as a proportion of the 1980s cycles. The proportional change was computed by dividing the difference between the 1992–2000 and 1978–1988 periods by the cycle from 1978 to 1988. Negative values indicate reduced abundance in the 1990s. Note: *C. finmarchicus* (a) and euphausiids (g) are plotted on a different scale.

and 1990s divided by the abundance in the 1980s (Figure 4). Compared with the 1980s, *C. finmarchicus* had a small proportional increase in the spring of the 1990s, but a decrease throughout the rest of the year, especially during autumn and

early winter. The change in *Centropages* abundance was strongest at the beginning of the year and is concentrated in two very large peaks in winter and late spring. As with *Centropages*, *Oithona* experienced its largest proportional



change at the beginning of the year (Figure 4c). In fact, the entire complex of taxa in the first PCA mode had large proportional increases during the winter period. This strongly suggests that the community shift resulted from a change in winter conditions in the Gulf of Maine.

It is interesting to consider the relationship between late-stage *C. finmarchicus* and the *Calanus* copepodites that are presumably the early life stages of *C. finmarchicus*. One might expect a strong association between these two taxa; however, the pairwise correlations suggest that they are largely independent. The correlation between the annual abundance anomalies of these taxa is not significant; rather, the *Calanus* copepodite time-series is more strongly correlated with each of the other taxa (Table 1). However, a careful examination of the entire *Calanus* pattern can shed some light on the larger patterns in the Gulf of Maine. As with the other taxa in the community shift pattern, the *Calanus* copepodites had their biggest proportional change between the 1980s and 1990s, during the early part of the year. Over the same period, late-stage *C. finmarchicus* had reduced abundance. Together, these suggest a period of elevated *Calanus* production during winter. This production led to an increase in late-stage *C. finmarchicus* abundance during late spring; however, the increase did not persist, and late-stage *C. finmarchicus* showed a decrease in abundance between 1980s and 1990s, during the summer.

#### Patterns in fish recruitment

The 12 fish stocks from the Gulf of Maine region exhibit a variety of patterns, reflecting the differences among the species and wide geographic range among the stocks

(Figure 5). A visual comparison between the recruitment series and the zooplankton principal components (Figure 2) does not reveal any obvious associations among the time-series. However, the statistical analyses did identify a number of significant correlations (Table 2).

The leading zooplankton mode captures the community shift pattern shared by many of the zooplankton taxa. This mode divides the period of interest into a low period (the 1980s) and a high period (the 1990s). Of the four fish stocks that are significantly correlated with this mode, most of the correlations are driven by the contrast between these two decades. The strongest linear correlation was between the leading zooplankton mode and Gulf of Maine yellowtail flounder ( $r = -0.70$ ,  $p < 0.01$ ). This stock had a string of good year classes centred around 1987, followed by a period of consistently low recruitment between 1989 and 1996, and two years of slightly stronger recruitment in 1997–1998. During the late 1980s, the leading zooplankton mode was consistently low, followed by the abrupt shift to higher values in 1990. This contrast between the 1980s and 1990s accounts for the negative correlation between this stock and the zooplankton mode. The recruitment of Gulf of Maine witch flounder was also significantly correlated with the leading zooplankton mode. The time-series for this stock was nearly the opposite of that for yellowtail, with steady, low recruitment through 1994 followed by a peak centred around 1997. This peak coincided with a steady increase in the zooplankton mode from 1995 until 2001. Recruitment of Georges Bank cod was relatively high during the 1980s, and with the exception of 1996 and 1998, it was low in the 1990s. This pattern is roughly the opposite of the

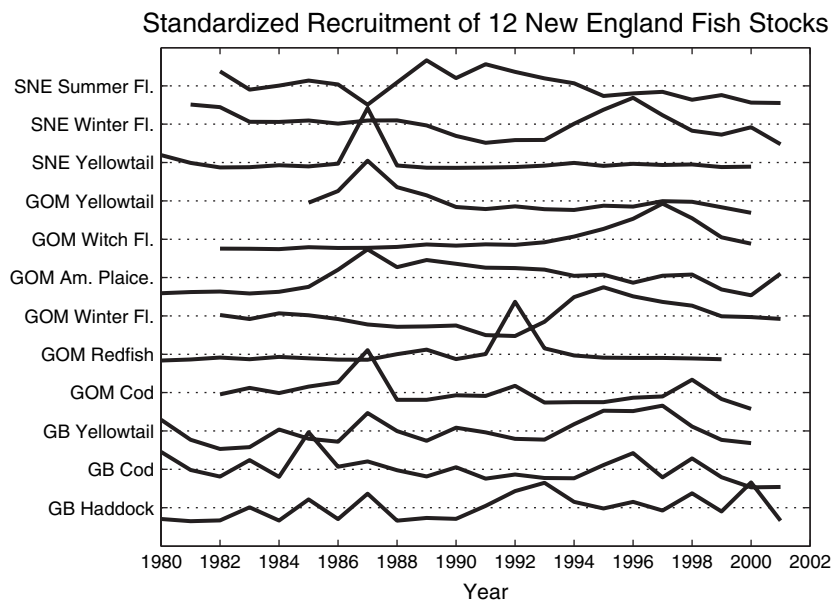


Figure 5. Recruitment of 12 fish stocks from the Gulf of Maine region. Each time-series represents the standardized recruitment (recruits/spawning stock, see text) normalized to have zero mean and unit variance. In the figure, the series are offset by three units.

Table 2. Correlations among recruitment in 12 fish stocks and the leading modes from the zooplankton principal component analysis. The stocks are from three regions: Georges Bank (GB), the Gulf of Maine (GOM), and southern New England (SNE). Each stock was compared with the two leading zooplankton modes using a standard linear correlation ( $r$ ) and a Spearman rank correlation ( $r_s$ ). Significant correlations are indicated by \* ( $p < 0.05$ ) and \*\* ( $p < 0.01$ ).

Species	Region	N	Mode 1 correlations		Mode 2 correlations	
			$r$	$r_s$	$r$	$r_s$
Haddock	GB	22	0.32	0.24	-0.43*	-0.41
Cod	GB	22	-0.52*	-0.57**	0.03	0.09
Yellowtail flounder	GB	21	0.14	0.05	0.10	0.05
Cod	GOM	19	-0.44	-0.43	0.31	0.26
Redfish	GOM	20	0.2	0.26	-0.03	0.12
Winter flounder	GOM	20	0.07	0.01	-0.16	-0.16
American plaice	GOM	22	0.05	0.06	0.35	0.41
Witch flounder	GOM	19	0.49*	0.73**	-0.28	-0.48*
Yellowtail flounder	GOM	16	-0.70**	-0.68**	0.66**	0.67**
Yellowtail flounder	SNE	21	-0.3	-0.21	0.34	0.01
Winter flounder	SNE	21	-0.46*	-0.54*	0.3	0.3
Summer flounder	SNE	20	-0.17	-0.15	0.2	0.14

zooplankton mode, and the two series are significantly negatively correlated ( $r = -0.52$ ,  $p < 0.05$ ;  $r_s = -0.57$ ,  $p < 0.01$ ). The only other stock exhibiting a correlation with the leading mode is winter flounder from southern New England. Recruitment of this stock declined in a nearly monotonic fashion from 1981 to 1993. Recruitment then increased, reached a peak in 1996, followed by a steady decline. The negative correlation with the zooplankton mode is driven by the steady decline in recruitment, with the 1996 peak appearing as an outlier.

The second zooplankton mode captures the variability in *C. finmarchicus*. Compared with the first mode, correlations between this mode and the fish stocks tended to be weaker. As with the first mode, the strongest correlations for the *Calanus* mode were found for the Gulf of Maine yellowtail stock ( $r = 0.66$ ,  $p < 0.01$ ;  $r_s = 0.67$ ,  $p < 0.01$ ). The positive correlations are driven by the peaks in abundance and recruitment centred around 1987, when *C. finmarchicus* abundance peaked. Georges Bank haddock had a weak but significant, negative correlation with the second mode ( $r = -0.43$ ,  $p < 0.01$ ). Several strong year classes for cod, notably 1993, 1998, and 2000, coincided with weak years in the *Calanus* mode, while some poor years for cod, including 1982, 1988, and 2001, were strong years in the *Calanus* mode. However, the many exceptions to this pattern led to a relatively weak relationship. Gulf of Maine witch flounder was the only other stock that was correlated with the second zooplankton mode ( $r_s = -0.48$ ,  $p < 0.05$ ). The period of low witch flounder recruitment followed by the 1997 peak appears as a strong linear trend when viewed as series ranks. Over this period, the *Calanus* mode tended to decline, reaching minimum rank values in 1998 and 1999. The trends in these time-series account for their weak negative rank correlation.

## Discussion

The time-series presented above provide a unique view of ecosystem changes in the Gulf of Maine. Previous studies using the CPR data either focused on *C. finmarchicus* (e.g. [Conversi et al., 2001](#); [MERCINA, 2001](#)) or used time-series that missed the 1990 shift (e.g. [Jossi and Goulet, 1993](#); [Licandro et al., 2001](#)). Our analysis indicates that there are two dominant patterns in the year-to-year changes in the Gulf of Maine zooplankton community, represented by the leading principal component modes ([Figure 2b](#)). The association between the zooplankton patterns and the recruitment of certain fish stocks suggests that the zooplankton data reflect large-scale changes in the Gulf of Maine ecosystem. Incorporating knowledge of these ecosystem-wide patterns successfully into fisheries management will require a mechanistic understanding of the processes leading to the changes. Specifically, we need to understand the processes that lead to interannual variability reflected by the two zooplankton principal component modes. The second mode is dominated by *C. finmarchicus*, and as the interannual variability of this species has been described earlier, our discussion will focus on the community shift.

### Community shift pattern

The leading mode from the PCA indicates that the Gulf of Maine witnessed a major ecological change between 1989 and 1990. This mode represents a fundamentally new pattern, one that has the potential to impact higher trophic levels, and it likely reflects other physical and biological changes in the region. The broad result of this change was an apparent increase in community diversity resulting from a shift away from *C. finmarchicus* towards smaller

taxa. The species that increased in 1989 have very different life histories and phenologies and occupy a range of ecological niches. For example, *Centropages* is a relatively large calanoid copepod that is most common in waters over the continental shelf (Kane, 1999), while *Oithona* is ubiquitous over the North Atlantic. Despite their large biological differences, the taxa represented in the community shift all had large proportional changes in their seasonal cycles during the winter–spring period (Figure 4). The concentration of the taxon-specific changes near the beginning of the year strongly indicates that the community shift is driven by processes during this portion of the year.

One of the community shift's unique features is the relationship between late-stage *C. finmarchicus* and *Calanus* copepodites during the 1990s. This relationship is characterized by an elevated abundance of early copepodites despite reduced adult abundance. We are fortunate that the late 1990s were one of the most intensively studied periods in the Gulf of Maine, due largely to field studies associated with the GLOBEC Georges Bank Programme. This research provided the foundation for a recent synthesis of *C. finmarchicus* population dynamics in 1998 and 1999 that described patterns strikingly similar to those described in this study (MERCINA, 2004). Physical oceanographic measurements collected during these studies can offer insight into possible mechanisms.

Early in 1998, the abundance of late-stage *C. finmarchicus* and younger copepodites was comparable with mean levels between 1995 and 1999; however, during summer, the abundance of late-stage *C. finmarchicus* declined dramatically. This decline has been attributed to reduced production in upstream regions on the Scotian Shelf or slope waters beyond the continental shelf, or reduced transport of individuals from these regions into the Gulf of Maine (MERCINA, 2004). The decline is also coincident with the arrival of cold Labrador Subarctic Slope Water associated with the 1996 drop in the NAO (MERCINA, 2001). The late summer *Calanus* crash resulted in very low abundance in the deep basins of the Gulf of Maine (MERCINA, 2004). However, a survey during February 1999 found increased abundance, relative to February 2000, of naupliar and early copepodite stages of most copepods, including *C. finmarchicus*, *Centropages*, and *Oithona* (Durbin *et al.*, 2003). The increase in copepod production was attributed to a winter phytoplankton bloom associated with a layer of relatively fresh Scotian Shelf Water.

The physical conditions in 1999 described by Durbin *et al.* (2003) led to an increase in the abundance of a wide range of zooplankton, and these conditions appear to be part of a larger-scale decadal change in the hydrography of the Northwest Atlantic. During the 1990s, surface salinity along the Northwest Atlantic Shelf, from Cape Hatteras to the Scotian Shelf, showed a marked decrease (Mountain, 2004). Smith *et al.* (2001) attributed this freshening to an increased freshwater and ice cover on the

Labrador Shelf. Looking more closely at the Labrador Sea, Häkkinen (2002) found that the surface waters there became dramatically fresher in the 1990s. The freshening was especially pronounced near the coasts. Unlike previous “Great Salinity Anomalies” (Belkin *et al.*, 1998), the event in the 1990s appears to have been independent of the NAO (Häkkinen, 2002).

The freshening of the surface waters of the Northwest Atlantic provides a possible mechanism to drive the 1989 community shift. As observed by Durbin *et al.* (2003), a decrease in salinity in the surface layer can stabilize the water column enough to support a phytoplankton bloom. The increased primary productivity associated with such blooms can support high copepod reproduction. Interannual differences in bottom temperature in deep basins of the Gulf of Maine provide further evidence of increased water column stability. Traditionally, strong cooling and intense mixing in the Gulf of Maine result in a very deep, mixed layer and pronounced cooling at depth, especially in the western portion of the Gulf (Brown and Irish, 1993). However, Mountain (2004) noted that the seasonal cycle of bottom water temperature was reduced in the 1990s, and he proposed that the surface freshening led to reduced winter convection.

If the freshening is indeed responsible for the zooplankton changes that we observed, then we would expect changes of a similar magnitude across the Northwest Atlantic Shelf. In addition to our zooplankton results, deYoung *et al.* (2004) noted an increase in “greenness”, an indicator of phytoplankton abundance, in the 1990s on the Newfoundland Shelf. Future work documenting the impact of this large-scale physical change would be an important contribution to our knowledge of the ecology of the Northwest Atlantic Shelf.

### *Calanus* pattern

Our proposal that the community shift pattern in the Gulf of Maine zooplankton community is driven by changes in winter productivity begs the question: why did late-stage *C. finmarchicus* decrease in the 1990s. One possible answer lies in this species' unique life history. Due to this species' preference for deep water during autumn and winter, shelf populations of *C. finmarchicus* are dependent on inputs from populations off the continental shelf (Greene and Pershing, 2001). Thus, unlike the other copepods whose abundance changes are likely attributable to *in situ* growth, *C. finmarchicus* will also be sensitive to changes in circulation. A good example of this comes from the Northeast Atlantic, where NAO-associated circulation changes play an important role in determining the abundance of *C. finmarchicus* in the North Sea (Heath *et al.*, 1999). Advective changes are also a leading hypothesis for the link between *C. finmarchicus* abundance in the Gulf of Maine and changes in the CSWS (Greene and Pershing, 2001; MERCINA, 2001, 2004).

## Ecosystem variability and fish recruitment

The correlation analysis presented above is a rough, initial attempt at understanding links between ecosystem changes in the Gulf of Maine and fish recruitment. Nevertheless, several significant correlations were found between the fish recruitment series and the two zooplankton modes. The strongest correlations were found between both zooplankton modes and witch and yellowtail flounder in the Gulf of Maine. The time-series for both stocks were dominated by large multi-year peaks, during the 1990s for witch flounder and the 1980s for yellowtail. For both of these stocks, the correlations were driven by a contrast between zooplankton conditions during the peak years and conditions in the low years, and it is possible that these correlations are artefacts of the peculiar structure of the recruitment series.

Fish recruitment is a complicated process that can be influenced by a variety of factors, and it is not surprising that the correlation between fish recruitment and zooplankton changes is not conclusive, despite evidence for large changes in the ecosystem. Spawning in most fish species occurs during certain portions of the year. Shifts in the timing of prey abundance relative to spawning can lead to recruitment variability (e.g. the “match–mismatch” hypothesis; Hjort, 1914; Cushing, 1990; Beaugrand *et al.*, 2003; Platt *et al.*, 2003), and shifts in timing are likely more important than average abundance like that measured by our yearly abundance series. Variability in the physical environment such as transport away from productive regions (Lough *et al.*, 1994) can also influence recruitment. If any of the correlations between zooplankton modes and recruitment represent real relationships, it is likely that the zooplankton modes function as proxies for a range of processes, both physical and biological. Future exploration will require more detailed modelling efforts to account for these factors (e.g. Brodziak and O’Brien, 2005).

## Conclusions

Our relatively simple analysis of zooplankton patterns in the Gulf of Maine identified two major modes of variability in this community. The dominant mode, which accounts for nearly two-thirds of the total variance, revealed a dramatic shift in community composition between 1989 and 1990 and a possible reversal in 2001–2002. In addition to the zooplankton changes, the 1990s were also a period of strong physical changes, most noticeably a large-scale freshening of the coastal waters from North Carolina to Newfoundland. The potential enhancement of winter stratification owing to the freshening could provide a bottom-up mechanism to explain the zooplankton changes. Although there were significant correlations between the zooplankton patterns and recruitment in some stocks, the impact of the zooplankton changes on upper trophic levels is still unclear and warrants further study.

## Acknowledgements

The authors thank the participants of the Climate-based Assessments and Forecasts for Ecosystems (CAFÉ) in the Gulf of Maine workshop held in June 2003 in Woods Hole, Massachusetts, especially David Mountain and Peter Smith. This work was supported by a Synthesis and Forecasting grant from NOAA’s Coastal Ocean Programme (award number NA17OP2666). Andrew Pershing’s travel to the symposium was provided by NSF.

## References

- Azarovitz, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. *Canadian Special Publications in Fishery and Aquatic Sciences*, 58: 62–67.
- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245–262.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Belkin, I. M., Levitus, S., Antonov, J., and Malmberg, S.-A. 1998. “Great Salinity Anomalies” in the North Atlantic. *Progress in Oceanography*, 41: 1–68.
- Brodziak, J., and Link, J. 2002. Ecosystem-based fishery management: what is it and how can we do it? *Bulletin of Marine Science*, 70: 589–611.
- Brodziak, J. K. T., and O’Brien, L. 2005. Do environmental factors affect recruits per spawner anomalies of New England groundfish? *ICES Journal of Marine Science*, 62: 1394–1407.
- Brown, W. S., and Irish, J. D. 1993. The annual variation of water mass structure in the Gulf of Maine: 1986–1987. *Journal of Marine Research*, 51: 53–107.
- Clark, R. A., Frid, C. L. J., and Batten, S. D. 2001. A critical comparison of two long-term zooplankton time-series from the central-west North Sea. *Journal of Plankton Research*, 23: 27–39.
- Conversi, A., Piontkovski, A. S., and Hameed, S. 2001. Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. *Deep Sea Research II*, 48: 519–520.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293.
- deYoung, B., Harris, R. P., Alheit, J., Beaugrand, G., Mantua, N., and Shannon, L. 2004. Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography*, 60: 143–164.
- Drinkwater, K. F., Petrie, B., and Smith, P. C. 2003. Climate variability on the Scotian Shelf during the 1990s. *ICES Marine Science Symposia*, 219: 40–49.
- Durbin, E. G., Campbell, R. G., Casas, M. C., Ohman, M. D., Niehoff, B., Runge, J., and 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.
- Francis, R. C. C., Hare, S. R., Hollowed, A. B., and Wooster, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, 7: 1–21.
- Greene, C. H., and Pershing, A. J. 2001. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation (NAO). *ICES Journal of Marine Science*, 57: 1536–1544.

- Greene, C. H., and Pershing, A. J. 2003. The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation. *Limnology and Oceanography*, 48: 319–322.
- Greene, C. H., and Pershing, A. J. 2004. Climate and the conservation biology of the North Atlantic right whale: the right whale at the wrong time? *Frontiers in Ecology and the Environment*, 2: 29–34.
- Greene, C. H., Pershing, A. J., Kenney, R. D., and Jossi, J. W. 2003. Impact of climate variability on the recovery of endangered North Atlantic right whales. *Oceanography*, 16: 96–101.
- Hare, S., and Mantua, N. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–145.
- Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J., and Schacht, A. 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, 8: 163–176.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. *Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer*, 20: 1–227.
- Häkkinen, S. 2002. Freshening of the Labrador Sea surface waters in the 1990s: another great salinity anomaly? *Geophysical Research Letters*, 29: 2002GL015243.
- Jossi, J. W., and Goulet, J. 1993. Zooplankton trends: US northeast shelf ecosystem and adjacent regions differ from northeast Atlantic and North Sea. *ICES Journal of Marine Science*, 50: 303–313.
- Kane, J. 1999. Persistent spatial and temporal abundance patterns for the late-stage copepodites of *Centropages typicus* (Copepoda: Calanoida) in the US Northeast Continental Shelf Ecosystem. *Journal of Plankton Research*, 21: 1043–1064.
- Licandro, P., Conversi, A., Ibanez, F., and Jossi, J. W. 2001. Time-series analysis of interrupted long-term data set (1961–1991) of zooplankton abundance in Gulf of Maine (Northern Atlantic, USA). *Oceanologica Acta*, 24: 453–466.
- Lough, R. G., Smith, W. G., Werner, F. E., Loder, J. W., Page, F. H., Hannah, C. G., Naimie, C. E., Perry, R. I., Sinclair, M., and Lynch, D. R. 1994. Influence of wind-driven advection on interannual variability in cod egg and larval distribution on Georges Bank: 1982 vs. 1985. *ICES Marine Science Symposia*, 198: 356–378.
- Mantua, N. J., and Hare, S. R. 2002. The Pacific decadal oscillation. *Journal of Oceanography*, 58: 35–44.
- Meise, C. J., and O'Reilly, J. E. 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 Research II*, 43: 1473–1501.
- MERCINA. 2001. Oceanographic responses to climate in the Northwest Atlantic. *Oceanography*, 14: 76–82.
- MERCINA. 2003. Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Progress in Oceanography*, 58: 301–312.
- MERCINA. 2004. Supply-side ecology and zooplankton populations' dynamics in the North Atlantic. *Oceanography*, 17: 60–71.
- Mountain, D. B. 2004. Variability of the water properties in NAFO subareas 5 and 6 during the 1990s. *Journal of Northwest Atlantic Fisheries Science*, 34: 103–112.
- Northeast Fisheries Science Center. 2002. Assessment of 20 northeast groundfish stocks through 2001. A report of the groundfish assessment review meeting (GARM), Northeast Fisheries Science Center, Woods Hole, MA, October 8–11, 2002. NEFSC Reference Document 02–16.
- Pershing, A. J., Greene, C. H., Planque, B., and Fromentin, J.-M. 2004. The influence of climate variability on North Atlantic zooplankton populations. *In Ecological Effects of Climatic Variations in the North Atlantic*, pp. 59–69. Ed. by N. C. Stenseth, G. Ottersen, J. Hurrell, and A. Belgrano. Oxford University Press.
- Platt, T., Fuentes-Yaco, C., and Frank, K. T. 2003. Spring algal bloom and larval fish survival. *Nature*, 423: 398–399.
- Rosby, T., and Benway, R. L. 2000. Low variations in mean path of the Gulf Stream east of Cape Hatteras. *Geophysical Research Letters*, 27: 117–120.
- Smith, P. C., Houghton, R. W., Fairbanks, R. G., and Mountain, D. B. 2001. Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993–97. *Deep Sea Research II*, 48: 37–70.
- Snedecor, G. W., and Cochran, W. G. 1989. *Statistical Methods*, 8th edn. Iowa University Press, Ames, IA.
- Taylor, A. H., and Stephens, J. A. 1998. The North Atlantic Oscillation and the latitude of the Gulf Stream. *Tellus*, 50: 134–142.
- Warner, A. J., and Hays, G. C. 1994. Sampling by the continuous plankton recorder survey. *Progress in Oceanography*, 34: 237–256.
- Wilks, D. S. 1995. *Statistical Methods in the Atmospheric Sciences: an Introduction*. Academic Press, San Diego, CA.