Update on the relationship between the North Atlantic Oscillation and *Calanus finmarchicus*

David G. Kimmel[1,3,*], Sultan Hameed[2]

[1]Horn Point Laboratory, University of Maryland Center for Environmental Science, 2020 Horns Point Road, Cambridge, Maryland 21613, USA

[2]Marine Sciences Research Center, The University at Stony Brook, Stony Brook, New York 11794-5000, USA

[3]*Present address:* Department of Biology/Institute for Coastal Science and Policy, East Carolina University, Greenville, North Carolina 27858, USA

ABSTRACT: The relationship between climate, represented by the North Atlantic Oscillation (NAO), and the calanoid copepod *Calanus finmarchicus* has been extensively studied. The correlation between NAO and *C. finmarchicus* has broken down (post-1995). In the present study, we revisit the relationship between *C. finmarchicus* and the NAO. Our reanalysis shows that previous treatment of this data did not take into account 2 aspects of both the *C. finmarchicus* and NAO index time-series: (1) the presence of significant trends and (2) significant autocorrelation. Our analysis suggests that previously reported relationships between NAO and *C. finmarchicus* abundance can be explained largely by the trends in both data series. Removing the trend from both time-series resulted in a decrease in the amount of *C. finmarchicus* abundance variability explained by the NAO. Trend removal eliminated the autocorrelation from the NAO time-series, but not from the *C. finmarchicus* time-series. Partial autocorrelation analysis showed that the autocorrelation present in the *C. finmarchicus* time-series is only found at a lag of 1 yr, suggesting strong, year-to-year connectivity in this population. We included the lagged *C. finmarchicus* abundance into a regression with the NAO and found that *C. finmarchicus* variability is explained by the previous year's abundance and, to a much smaller extent, by NAO variability. Limiting the time-series to the most recent 22 yr period (1981 to 2002) showed that the NAO is no longer correlated to *C. finmarchicus* abundance, and the autocorrelation in the *C. finmarchicus* abundance series also appears to be weakening.

KEY WORDS: North Atlantic Oscillation · *Calanus finmarchicus* · Trend · Autocorrelation · Time-series

INTRODUCTION

The relationship between climate variability and marine organisms has long been recognized (Cushing & Dickson 1976). Interest in this subject has typically centered on large spatial-scale climate indices, e.g. the North Atlantic Oscillation (NAO), El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). Strong relationships have been found among the NAO (Ottersen et al. 2001, Parsons & Lear 2001), ENSO (Pearcy & Schoener 1987, Sugimoto et al. 2001), PDO (Hollowed et al. 2001, Royer et al. 2001) and the abundance of various marine organisms. In particular,

shifts in plankton abundance in relation to climate indices have been well studied in the northeast Atlantic Ocean (e.g. Taylor 1995, Fromentin & Planque 1996, Planque & Reid 1998, Planque & Taylor 1998).

The dominant mesozooplankton species across much of the northeast Atlantic Ocean is the calanoid copepod *Calanus finmarchicus*. Using Continuous Plankton Recorder (CPR; see Jossi et al. 2003) data for the period 1962 to 1992, Fromentin & Planque (1996), suggested that long-term changes in *C. finmarchicus* abundance in the northeast Atlantic were strongly coupled to the NAO. Planque & Taylor (1998) further extended these analyses by using the position of the

Gulf Stream north wall, as well as the NAO, to predict *C. finmarchicus* abundance. Planque & Reid (1998) developed a linear regression model between *C. finmarchicus* abundance and the NAO for the years 1958 to 1992. Their goal was to use this model to predict *C. finmarchicus* abundance for 1993 to 1997. They reported that the predictions for 1993 to 1995 were close to the observed values, but found a sharp discrepancy between observations and predictions for the years 1996 to 1997 (Planque & Reid 1998). *C. finmarchicus* abundance and NAO index variability have continued to deviate from each other (Fig. 1).

In the present study, we revisit the relationship between *Calanus finmarchicus* and the NAO. Our results suggest that the coupling between the NAO and *C. finmarchicus* is weaker than has been assumed in previous literature. The impact of the prior year's *C. finmarchicus* population is the dominant factor in determining the size of the current year's abundance with a small contribution due to NAO-related environmental variability.

MATERIALS AND METHODS

Zooplankton data were acquired from the Sir Alister Hardy Foundation for Ocean Science and were collected using the CPR (Jossi et al. 2003, Richardson et al. 2006). The area covered by these data can be seen in Fromentin & Planque (1996, their Fig. 1). We used the same data as Planque & Fromentin (1996), which consisted of stage V copepodites and adult *Calanus finmarchicus* abundance. The data were log-transformed $(x + 1)$ prior to analysis. The annual values used were the mean abundance from January to December (Planque & Fromentin 1996).

The NAO is defined as the difference in normalized sea level pressure (SLP) between Lisbon, Portugal, or Ponta Delgada, Azores, and Stykkisholmur/Reykjavik, Iceland (Hurrell 1995). The winter (December through March) index of the NAO based on the difference of normalized SLP between Lisbon and Stykkisholmur/Reykjavik is available at: www.cgd.ucar.edu/cas/jhurrell/indices.html and was used in the present study. All statistical analyses were performed using S-PLUS (Insightful, see www.insightful.com/products/splus) software package.

RESULTS

Correlation between NAO and *Calanus finmarchicus* abundance for the period 1958–2002 is –0.54, i.e. it explains ca. 25% of the copepod variance (Table 1). When we limit the copepod data to 1958–1992, the correlation with the NAO index is –0.71, similar to the value –0.76 reported by Planque & Reid (1998) for the period 1958–1995. Thus, there is a substantial decrease in correlation when the copepod data are extended from 1995–2002. If the time-series is further separated into 2 equal segments (1958–1980 and 1981–2002), the correlation between *C. finmarchicus* and NAO is significant for the first time period, but not the latter (Table 1).

The *Calanus finmarchicus* abundance has been in a general downward trend during the period of the present study (Fig. 1). This trend is significant for the time periods 1958 to 2002 and 1958 to 1992 (Table 1). The years 1958 to 1980 also had a negative trend, though it was not significant because of the rise in *Calanus* during 1976 to 1980 (Table 1, Fig. 1). The NAO also had a significant, positive trend during the 1958 to 2002 and 1958 to 1992 time periods (Table 1). The trend was not present during either of the 2 halves of the data. The NAO has departed from its earlier upward trend (Fig. 1). We removed the trend from the *C. finmarchi-*

Table 1. Correlation, trend and autocorrelation estimates for *Calanus finmarchicus* abundance (*C. fin*) and NAO index and after removal of linear trends using least squares regression. p-values are given in parentheses; values in bold represent significant values with p < 0.05

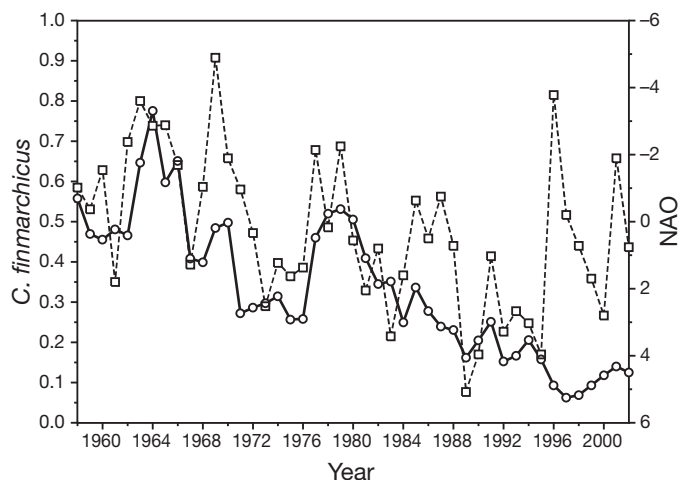| Time period	Trend Kendall's τ		Autocorrelation Yule-Walker AR(1) ρ		Correlation Pearson's R
	C. fin	NAO	*C. fin*	NAO	*C. fin* vs. NAO
1958–2002	**−0.67 ($1 \times 10^{−10}$)**	**0.31 (0.002)**	**0.85 ($1 \times 10^{−8}$)**	**0.40 (0.008)**	**−0.54 (0.0001)**
1958–1992	**−0.53 ($7 \times 10^{−6}$)**	**0.38 (0.001)**	**0.74 (0.00001)**	**0.47 (0.005)**	**−0.71 ($1 \times 10^{−6}$)**
1958–1980	−0.20 (0.18)	0.17 (0.27)	**0.67 (0.001)**	0.31 (0.13)	**−0.64 (0.001)**
1981–2002	**−0.70 ($5 \times 10^{−6}$)**	−0.08 (0.61)	**0.74 (0.0005)**	0.12 (0.56)	0.11 (0.61)
After trend removal					
1958–2002	0.03 (0.81)	0.03 (0.76)	**0.60 (0.00005)**	0.24 (0.10)	**−0.34 (0.02)**
1958–1992	0.04 (0.71)	0.17 (0.15)	**0.59 (0.0004)**	0.29 (0.08)	**−0.48 (0.003)**
1958–1980	0.07 (0.67)	0.0004 (1)	**0.60 (0.004)**	0.26 (0.21)	**−0.58 (0.003)**
1981–2002	−0.22 (0.16)	−0.23 (0.14)	0.31 (0.15)	0.21 (0.32)	0.05 (0.25)

Fig. 1. *Calanus finmarchicus*. Comparison of copepod abundance from the Continuous Plankton Recorder (CPR) data set used by Fromentin & Planque (1996) (○) with the winter (December to March) North Atlantic Oscillation (NAO) index (Hurrell 1995) (□). NAO is shown on an inverted scale

cus and NAO time-series using linear regression. The residuals for both time-series did not show a significant trend (Table 1). The trend removal resulted in a decrease in the strength of the correlation between *C. finmarchicus* and NAO during the time periods 1958 to 2002 and 1958 to 1992 (Table 1). The NAO explained 29% of the variance in *C. finmarchicus* abundance with the trends present in both data for the time period 1958 to 2002 (Table 1, Pearson's r = −0.54). After trend removal, the NAO explained only 12% of the variance (Table 1; Pearson's r = −0.54) for the same time period. The correlation between *C. finmarchicus* and the NAO was significant for only the first half of data, 1958 to 1980 (Table 1). Thus the correlation between these 2 variables is dominated by their trends, i.e. it was high earlier and has decreased in the latter half of the data set.

The *Calanus finmarchicus* and NAO time-series are also autocorrelated (Table 1). The NAO is autocorrelated during 1958 to 1992 and for the whole period 1958 to 2002, whereas *C. finmarchicus* abundance is autocorrelated during all time segments (Table 1). After trend removal, the autocorrelation at lag 1 in *C. finmarchicus* remained strong, while the autocorrelation in the NAO time-series was no longer present (Table 1). *C. finmarchicus* autocorrelation was not significant during the time period 1981 to 2002 (Table 1). We used the partial autocorrelation function (PACF) to differentiate between autocorrelations in *C. finmarchicus* abundance and in the NAO. The PACF is an extension of the correlation function where the dependencies on the intermediate lags are removed (Shumway & Stoffer 2000). A statistically significant

correlation between the NAO and itself lagged 1 yr was present for the entire time period (1958 to 2002) (Table 1). This trend and a significant correlation at a lag of 5 yr (r = 0.38, p = 0.05) can be interpreted as a quasi-oscillation of this period in the NAO (Fig. 2a). *C. finmarchicus* also shows an autocorrelation at lag 1, but it is much stronger than that of the NAO (Table 1, Fig. 2b). This indicates a stronger autocorrelation than in the NAO, and lack of other significant lags indicates the lack of multi-year oscillation in the *C. finmarchicus* time-series. The autocorrelation of 0.88 with 1 yr lag suggests another possibility for explaining the variation in C. *finmarchicus* abundance.

Calanus finmarchicus with 1 yr lag and the NAO can be used as independent variables in a linear regression equation as they are not correlated for any time period (Pearson's r = −0.28 to 0.14, p > 0.21). The regression equation for the time period 1958 to 2002 is:

$$Cf = 0.0009 + 0.5739(Cf_{lag1yr}) - 0.0131(NAO) \quad (1)$$

where Cf is *C. finmarchicus* abundance residuals after trend removal, Cf_{lag1yr} is *C. finmarchicus* abundance residuals for the previous year after trend removal and NAO is the December to March value of the NAO index residuals after trend removal. The p-values of the regression coefficients are all less than 0.05. The majority of the variance in *C. finmarchicus* abundance
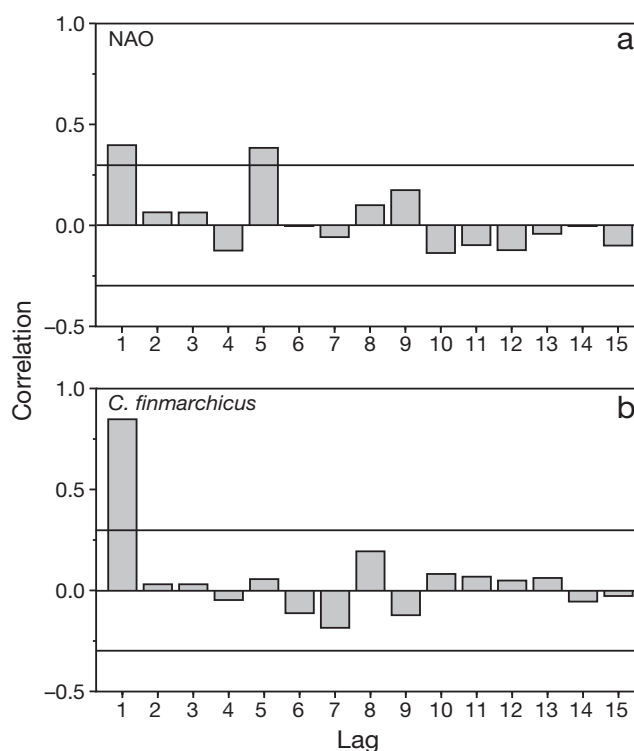

Fig. 2. Partial autocorrelation at multiple lags for the (a) NAO and (b) *Calanus finmarchicus* abundance. Horizontal black lines: 95% confidence interval

is explained by the previous year's abundance (semi-partial $r^2 = 0.36$) and not the NAO (semi-partial $r^2 = 0.08$). *C. finmarchicus* abundance residuals calculated by this regression compared well with the observed abundance residuals from 1958 to 2002 (Fig. 3). This result is a significant improvement on a regression using the NAO index as the lone predictor variable (Table 2). The same regression equation for the time period 1958 to 1992 explained 51% of the variance in *C. finmarchicus* abundance residuals (Table 2). Both subperiods of data had significant regression equations and explained at least 26% of the variance in *C. finmarchicus* abundance. All of this explained abundance in the 1981 to 2002 time period was a function of the prior year's *C. finmarchicus* abundance (Table 2).

DISCUSSION

The detection of causal relationships between 2 time-series is not straightforward. Ecological time-series are often non-stationary, i.e. they possess a trend or have serial autocorrelation (Jassby & Powell 1990). The presence of either can obscure relationships be-
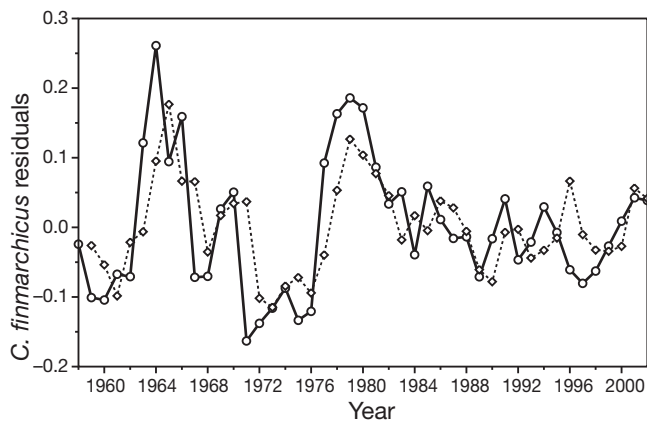

Fig. 3. *Calanus finmarchicus*. Time-series of the residuals of copepod (O) abundance after trend removal and *C. finmarchicus* residuals predicted (◇) from the regression model in the text

tween 2 time-series or produce relationships between time-series that are spurious. Our findings show that the relationship between NAO and *Calanus finmarchicus* abundance in the northeast Atlantic is weaker than previously thought. The strong correlation between *C. finmarchicus* abundance and the NAO shown by Fromentin & Planque (1996) was largely the result of opposing trends present in both time-series. Fromentin & Planque (1996) noted that trends were present in the data and performed trend removal in the NAO data set using a third-order, polynomial fit. However, they did not remove the significant trend present in the *C. finmarchicus* abundance time-series (Table 1). In addition to the presence of a trend, both time-series showed significant autocorrelation (Table 1). After trend removal using least-squares regression, the autocorrelation in the NAO time-series was no longer present; however, the *C. finmarchicus* time-series remained significantly autocorrelated (Table 1). This, coupled with a partial autocorrelation analysis that revealed autocorrelation in the *C. finmarchicus* abundance occurring only at a lag of 1 yr, suggested that interannual variability in *C. finmarchicus* is largely a function of the prior year's abundance. There are other reported examples where the previously postulated couplings of phenomena over the North Atlantic with the NAO have deteriorated as the NAO trend has changed direction since the mid-1990s. This was noted for the Gulf Stream northwall by Hameed & Piontkovski (2004) and for the export of Saharan dust to the Atlantic Ocean by Riemer et al. (2006).

We found that the significant autocorrelation present in the *Calanus finmarchicus* time-series could be used in a regression equation. By including the prior year's abundance of *C. finmarchicus* into the regression between NAO and *C. finmarchicus* abundance, we found a significant relationship. This relationship matched the *C. finmarchicus* abundance closely including in the years post-1996, when it appeared that the relationship between *C. finmarchicus* and NAO had broken down (Fig. 3). However, when data were limited to the most recent 22 yr period (1981 to 2002), the addition of the NAO into the regression equation did not explain any additional variance in *C. finmarchicus* abundance. The prior year's abundance was still able to explain a statistically significant fraction of the variance in *C. finmarchicus* abundance (26%); however, it appears that the auto-correlation in the time-series has significantly weakened.

The tight coupling seen between *Calanus finmarchicus* in adjacent years is most likely a result of the number of *C. finmarchicus* that enter dor-

Table 2. Linear regression coefficients of determination (r^2) and model p-values for various regression equations: (1st column) *C. fin* = a(NAO) + c; (2nd column) *C. fin* = a(*C. fin.* lag 1 yr) + c; (3rd column) *C. fin* = a(*C. fin.* lag 1 yr) + b(NAO) + c. Bold values are significant at $p < 0.05$. a and b are regression coefficients and c is the intercept

Time period	NAO	*C. fin.* lag 1 yr	NAO + *C. fin.* lag 1 yr
1958–2002	**0.12 (0.02)**	**0.36 (0.0001)**	**0.44 (6×10^{-6})**
1958–1992	**0.23 (0.003)**	**0.36 (0.0002)**	**0.51 (0.00001)**
1958–1980	**0.34 (0.003)**	**0.39 (0.002)**	**0.57 (0.0003)**
1981–2002	0.003 (0.81)	**0.27 (0.01)**	**0.26 (0.05)**

mancy in the fall and overwinter. *C. finmarchicus*, similar to other calanoid species, survives winter conditions by entering a dormant state characterized by low metabolic demand (Dahms 1995). The CV stage copepodites migrate to depth and lie dormant until spring (Hirche 1996). Emergence from dormancy appears to be related to photoperiod (Speirs et al. 2006), with a possible secondary trigger that causes arousal at depth (Miller et al. 1991). However, recent work suggests that no single environmental cue consistently explains entry or emergence from dormancy (Johnson et al. 2008). The primary mechanism determining entry into dormancy was hypothesized to be a function of the ability of individual *C. finmarchicus* to accumulate adequate lipid reserves (termed the lipid accumulation window hypothesis) (Johnson et al. 2008).

Exit from dormancy is thought to be a function of lipid consumption (Saumweber & Durbin 2006). Saumweber & Durbin (2006) predicted emergence from dormancy for *Calanus finmarchicus* populations in the Gulf of Maine based on animal length, oil sac volume and *in situ* temperature. They suggest that temperature is the primary environmental determinant because it regulates metabolic consumption of lipid stores, thereby forcing copepods to emerge from dormancy when the energy stored in these lipids is exhausted. Heath et al. (2000) concluded that seasonal cycles of food and temperature, combined with a proximity to overwintering habitats, determined the productivity of *C. finmarchicus* locally. It is this locally produced *C. finmarchicus* population that enters dormancy during the fall after accumulation of sufficient lipid reserves and thereby determines, to a large degree, the abundance for the next year.

It now appears that the strong connection between year-to-year populations of *Calanus finmarchicus* is weakening. This may be due to a variety of factors. For instance, the population of *C. finmarchicus* in the northeast Atlantic may have been pushed in one direction by long-term trends in local production that are related to temperature. *C. finmarchicus* is typically found in lower temperatures and is considered an indicator of the Artic Polar Biome (Helaouet & Beaugrand 2007). *C. finmarchicus* growth and development are coupled to temperature (Sundby 2000, Campbell et al. 2001); therefore, a long-term increasing trend in temperature may explain the long-term decline in *C. finmarchicus* populations. Levitus et al. (2005) presented data on increases in heat content of the oceans from surface to 3000 m depth for 1955 to 2003. Their results show that the North Atlantic water mass is heating faster than any of the other basins. The 1000 to 3000 m layer of the North Atlantic added 1.3×10^{22} J of heat during this period. The analysis of Levitus et al. (2005) is for the entire North Atlantic, but it suggests that a
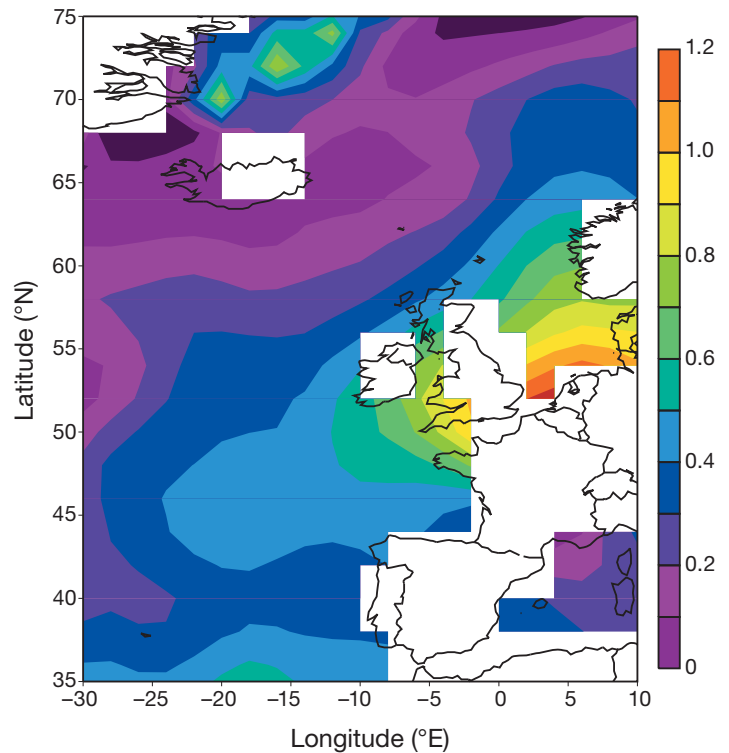

Fig. 4. Sea surface temperature (SST, °C) differences between the time periods 1998 to 2002 and 1950 to 1954. Note all differences are positive, indicating a warming trend since 1950

significant warming trend is taking place in the deep ocean of the CPR region where *C. finmarchicus* overwinters. There have also been changes in sea surface temperature (SST) over the CPR region between two 5 yr periods (1950 to 1954 and 1998 to 2002), using NOAA's extended SST data set (Fig. 4). It shows that the surface has warmed throughout the region. Heath et al. (1999) proposed that the decline of *C. finmarchicus* abundance was a result of a reduction in overwintering habitat available due to a decrease in the volume of Norwegian Sea Deepwater. Warm-water zooplankton species have become prevalent in this region (Beaugrand et al. 2002, Beaugrand 2003). However, other factors, such as natural mortality and mortality due to predation, may be causing the breakdown (Ohman et al. 2004). While it is unclear what is driving this long-term decline in the *C. finmarchicus* population in the northeast Atlantic, it is apparent that it has uncoupled *C. finmarchicus* abundance from the NAO.

CONCLUSIONS

A reexamination of the *Calanus finmarchicus*–NAO relationship shows that the correlation between the 2 time-series was largely the result of

trends present in both series. The correlation between *C. finmarchicus* and NAO remained significant after trend removal; however, the presence of autocorrelation in the *C. finmarchicus* abundance time-series remained. We used this autocorrelation in a regression model and found that it explained the majority of year-to-year variability in *C. finmarchicus* abundance. We suggest that the connectivity between *C. finmarchicus* populations in adjacent years is a function of the overwintering CV copepodites. After trend removal, and accounting for autocorrelation, the NAO still explains a small, but statistically significant, portion of the variance in *C. finmarchicus* abundance. Examination of a more recent time period (1981 to 2002) revealed that the NAO no longer explains variance in *C. finmarchicus* abundance and that though the prior year's abundance of *C. finmarchicus* still explained a significant portion of the variance in *C. finmarchicus* abundance, this relationship appeared to be weakening. We suggest that the weakening connection between year-to-year populations of *C. finmarchicus* in the northeast Atlantic may be a function of long-term warming of the northeast Atlantic or other factors, such as mortality, that are more difficult to quantify.

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