

Multi-decadal range changes vs. thermal adaptation for north east Atlantic oceanic copepods in the face of climate change

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Abstract

Populations may potentially respond to climate change in various ways including moving to new areas or alternatively staying where they are and adapting as conditions shift. Traditional laboratory and mesocosm experiments last days to weeks and thus only give a limited picture of thermal adaptation, whereas ocean warming occurring over decades allows the potential for selection of new strains better adapted to warmer conditions. Evidence for adaptation in natural systems is equivocal. We used a 50-year time series comprising of 117 056 samples in the NE Atlantic, to quantify the abundance and distribution of two particularly important and abundant members of the ocean plankton (copepods of the genus *Calanus*) that play a key trophic role for fisheries. Abundance of *C. finmarchicus*, a cold-water species, and *C. helgolandicus*, a warm-water species, were negatively and positively related to sea surface temperature (SST) respectively. However, the abundance vs. SST relationships for neither species changed over time in a manner consistent with thermal adaptation. Accompanying the lack of evidence for thermal adaptation there has been an unabated range contraction for *C. finmarchicus* and range expansion for *C. helgolandicus*. Our evidence suggests that thermal adaptation has not mitigated the impacts of ocean warming for dramatic range changes of these key species and points to continued dramatic climate induced changes in the biology of the oceans.

Keywords: climate change, long-term changes, top down control, bottom up control, NAO, sea surface temperature, copepods, Mesozooplankton, westerly wind

Received 24 June 2013; revised version received 20 August 2013 and accepted 22 August 2013

Introduction

Climate change is having profound impacts on the phenology, abundance and distribution of a broad range of taxa across both marine and terrestrial systems (Thackeray *et al.*, 2008; Falkowski, 2012). How these demographic processes will change in the future is one of the burning questions in ecology and has very wide socioeconomic implications. Habitat suitability models have been widely used to try and predict how species ranges might change in the future. These models tend to use empirical observations to formulate a multivariate statistical representation of a species niche by relating species distributions to key environmental variables (e.g. temperature, rainfall,

humidity) and then using predictions from the Intergovernmental Panel of Climate Change (IPCC), or elsewhere, for how the environmental variables will change over future decades in order to predict the corresponding future species range changes (Guisan & Thuiller, 2005). However, in their simplest form such models may have limited utility as they ignore the adaptive potential of species. This assumption of niche conservatism has been challenged (Losos, 2008; Pearman *et al.*, 2008) and indeed there is some evidence that species may adapt to changing conditions (Lavergne *et al.*, 2010). For example, there is strong evidence for both between and within population variation for traits that make up species ecological niches, that is, individuals are often adapted for their local conditions suggesting the potential to adapt to new conditions as the climate changes (Savolainen *et al.*, 2007). Often temperature is one of the most important components of climate change and drivers of species

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distribution. As part of this focus on environmental temperature, thermal performance curves (TPCs) describe the relationships between temperature and biological rate processes and manipulative experiments in laboratory conditions or mesocosms have shown rapid microevolutionary modifications of TPCs to changing conditions (Schulte *et al.*, 2011). There is therefore evidence that niche conservatism may not be as widespread as previously assumed. Many of these studies, however, use exposures to constant extreme temperatures as the selective agent, so their relevance to the effects of anthropogenic climate change remains unclear and current understanding of the mechanisms underlying the responses of organisms to temperature change is incomplete.

In the oceans the pace of warming is larger than in terrestrial environments, as evidenced by the rate of polar movement of isotherms over recent decades (Richardson & Schoeman, 2004). These environmental changes suggest that changes in species abundance and distribution may be most marked in marine systems (Brown *et al.*, 2011), a prediction that seems to be matched by empirical evidence (Parmesan & Yohe, 2003). For example, in response to rising water temperatures, warm-water plankton species are showing an expanded range in the NE Atlantic and colder water species a corresponding range contraction (Beaugrand *et al.*, 2002, 2009). A key unresolved question is how species might adapt to rapidly rising sea temperatures and if any adaptation will mitigate projected range changes.

Materials and methods

CPR survey

Continuous Plankton Recorder (CPR) samples are collected from ships-of-opportunity that tow a robust plankton filtering instrument at a depth of 6–7 m (Hays, 1994), and due to the mixing of the ship the CPR samples the 0–20 m surface layer (Hunt, 1969). Therefore, changes in the abundance of *Calanus* are based on the subsurface distribution of the species. For further information regarding the technical background, consistency and comparability of CPR sampling see Richardson *et al.* (2006).

CPR data for *C. finmarchicus* and *C. helgolandicus* from 1960 to 2010 ($n = 117\,056$) (Johns, 2012) were examined within seven areas of the North Atlantic: NE Atlantic (20°W–8°E, 45–64°N), southern North Sea, northern North Sea, north west Scotland sector, north west Atlantic approaches, Irish Sea, and the south west Atlantic approaches (Fig. S1). These regions were chosen based on Planque & Batten (2000), who concluded that long-term patterns of *C. finmarchicus* variability are region specific and Beaugrand (2009) who suggested the need for more localized analysis of ecosystem shifts.

Large scale hydro climatic parameters

The winter North Atlantic Oscillation Index (NAOI) for the period 1960–2010 was used, where the 1960 value is represented by December of 1959 and January to March of 1960. The NAOI is calculated as the normalized difference in winter sea-level pressures between Stykkisholmur in Iceland and Lisbon in Portugal (Hurrell *et al.*, 2001) (<http://www.cgd.ucar.edu/cas/jhurrell/>).

Monthly mean gridded (1°×1°) sea surface temperature (SST) and westerly wind speed (m s^{-1}) data from 1960 to 2010 were obtained from Hadley Centre of the UK Met Office (HADISST) (<http://www.metoffice.gov.uk/hadobs/hadisst/>) (Rayner *et al.*, 2003) and The International Comprehensive Ocean-Atmosphere Data Set (ICOADS) (<http://www.ncdc.noaa.gov/oa/climate/coads/>) respectively. Data are summarized for a given latitude and longitude. Annual SST and westerly wind speed averages were calculated for the NE Atlantic region (45–64°N; 20°W–8°E), and for the areas A–F (Fig. S1).

Spatial maps of individual taxa

Data derived from 117 056 CPR samples were used to create maps showing the general spatial distribution and relative abundance of *C. finmarchicus* and *C. helgolandicus* between 1960 and 2010 in an area 20°W–8°E and 45–64°N. Maps were calculated using an ordinary kriging method, which was carried out using the packages “sp” (Pebesma & Bivand, 2005) and “gstat” (Pebesma, 2004) within R (R, 2009). One of the assumptions of kriging is that spatial structures are stable over the duration of the sampling period (Simard *et al.*, 1992), which was clearly not the case for CPR data collected over a period of 51 years. To address this issue, when producing spatial maps the data sets were partitioned into shorter temporal periods (Edwards, 2000). For each individual taxa, the abundance data were firstly split into approximately 5-year intervals (1960–1964, 1965–1969, 1970–1974, 1975–1979, 1980–1984, 1985–1989, 1990–1994, 1995–1999, 2000–2004, 2005–2010). For each time period, data were split into months where kriging was applied to produce twelve maps. Finally, for each taxa and decadal time period, a singular composite map was produced by averaging each grid node over the 12 months (see Hinder *et al.* (2012) for further description of methodology).

Relationship between abundance and environmental variables

The average yearly abundance for *Calanus* over a given geographical area (NE Atlantic or areas A–F) was compared to the corresponding (average) changes in SST, westerly wind speed and the NAOI in a set of correlation and regression analyses. We employed a range of statistical methods that address different sources of spurious correlation that can arise in ecology time series analysis. We initially used Pearson Correlation to test the relationships between the three climate variables and *Calanus* taxa. However, a problem with

long-term data is one of serial autocorrelation (that is often present in ecological time series), which can lead to high type I error rates in correlation analysis (Yule, 1929). We controlled for this autocorrelation by using the 'modified Chelton method' (Pyper & Peterman, 1998).

We further tested for long-term links between variables with 'causal' methods borrowed from econometrics. The criteria for Granger causality are that forecasting of future values of a target variable is significantly improved by past observations of a causal variable after adjustment for past values of the target variable. This can be achieved in a standard regression framework, using lagged values of the target and putative causal factor as predictors (Thurman & Fisher, 1988). All variables were time detrended initially, by extracting the residuals from regression models, as non-stationary time series can lead to spurious results. A range of plausible lags were investigated and statistical significance was assessed by comparing models with/without the putative causal factor using likelihood ratio tests. This represents a test of the link between environmental and distribution variables over and above that provided by correlation alone (since lagged values of the target variable are included in the regression themselves) (see Data S1).

Similarly, cointegration can be used to tease out genuine links between time series beyond the simple correlation that is often induced by common short-term time trends, and hence be used as a cross check on the Granger models. If, for time series processes of a given order of integration, there exists a linear combination of the series that has a lower order of integration, the two series are considered to be cointegrated. As such, cointegrated time series have trajectories that are intimately linked and unlikely to diverge (Phillips and Ouliaris 1990). The presence of cointegration indicates a true long-term relationship is more likely, and also directly implies Granger causality in one or other direction (though the converse is not true). Cointegration models were fitted using the R function `po.test` (Phillips and Ouliaris 1990).

Results

We used the longest plankton time series in existence, the CPR data spanning 50 years, to explore how the relationships between the abundance of key plankton and environmental conditions have changed over recent decades. We examined changes in abundance for two key species, *C. finmarchicus* and *C. helgolandicus*, which play important roles as food for fish and so drive bottom up control of important commercial fisheries. Clear changes in the distribution and abundance of *Calanus* in the NE Atlantic region (Fig. 1) have been observed. *C. finmarchicus* was maximally abundant in the Norwegian Sea off northern Scotland in the 1960s–1980s, but there have been dramatic declines in abundance in these areas in the last two decades. The abundance of *C. helgolandicus* has generally followed the reverse pattern (Fig. 1). In some areas, *C. helgolandicus* has been relatively abundant throughout the time series (e.g. south west of the United Kingdom), while in other areas (generally further north) there has been a progressive increase in abundance such as off northern Scotland and in the northern North Sea.

Over the last few decades, significant correlations have been identified between the abundance of these species and various environmental drivers, including wind speed, the NAOI and SST. We explored how the strengths of these correlations have changed as time series have lengthened to try and identify the key environmental drivers underlying abundance changes and hence explore the robustness of using environmental correlates to predict future plankton changes. By exploring how abundance vs. environmental conditions

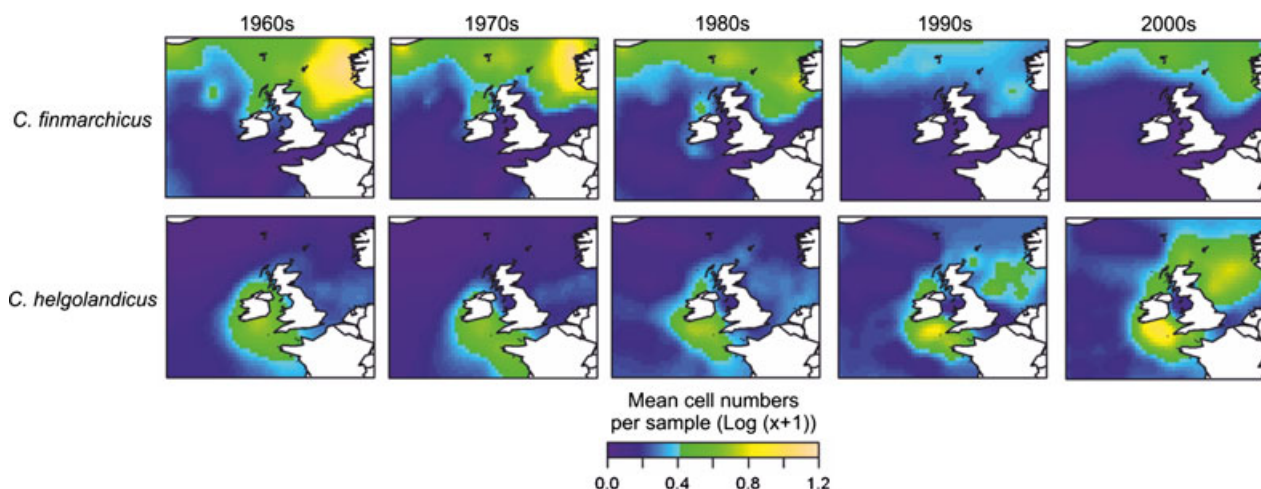


Fig. 1 Decadal spatio-temporal changes in the abundance of *C. finmarchicus* and *C. helgolandicus*. Colour scale represents decadal mean number of individuals per sample [$\log(x+1)$].

have changed over time we consider if there is any evidence for adaptation to warming seas and how any adaptation has mitigated observed range changes. To do this, we first considered the years 1960–1992, (based on Fromentin & Planque (1996)), and tested for significant relationships between *Calanus* abundance and both SST, the NAOI and westerly wind speed using Pearson correlation and after adjusting for serial autocorrelation using the modified Chelton method (Pyper & Peterman, 1998). The time series was progressively extended by 1 year until the full time series (1960–2010) was analysed.

This analysis showed how initially when the *Calanus* abundance time series was 32 years long, the abundance of *C. finmarchicus* and *C. helgolandicus* were both significantly correlated with both westerly wind speed and the NAOI (negatively correlated for *C. finmarchicus* and positively correlated with *C. helgolandicus*) (Fig. S2, S3 and Table S1). However, as the time series lengthened, the significant correlations with the NAOI and westerly wind speed weakened while at the same time the correlations between *Calanus* abundance and SST have strengthened. These changing relationships reflect the patterns of the NAOI and SST, with both variables initially covarying until the mid-1980s, after which their trends differed.

We tested for Granger causality, where past values of a putative causal environmental variable (SST, westerly wind speed, and the NAOI) are used in a regression model to predict future values of *Calanus* abundance after adjusting for past values of *Calanus* abundance (Thurman & Fisher, 1988). This approach represents a measure of forecasting over and above that provided simply by past temporal changes, and helps point towards a causal link (Thurman & Fisher, 1988). This analysis showed little evidence for Granger causality for either species against SST, the NAOI and westerly wind speed. Although there was evidence for a significant Granger causality in the NE Atlantic and north west Atlantic approaches for *C. helgolandicus* against SST appearing over a lag of 1 year and 2 years respectively ($P = 0.03$ and $P = 0.03$, Table S2). This result was consistent with estimates of cointegration, which was significant at the 10% level ($P = 0.076$). No significant Granger causality was found for *C. finmarchicus*, although there was some small indication of cointegration ($P = 0.15$). No evidence for cointegration or Granger causality was found for the NAOI (Table S2).

To look carefully for any evidence of adaptation within the decadal data, for each decade we generated an SST/abundance response curve by plotting mean observations across different regions (see Fig. S1 for definition of regions). We tested for adaptation by comparing the fit of a model that assumes a constant

relationship between SST and abundance with one that fits each decade separately. We used linear regression models, with quadratic terms as required. The fit of competing models was compared with likelihood ratio tests, and the regression slopes investigated for evidence of changes in the relationship between abundance and SST over time.

The decadal interregional relationships between *C. finmarchicus* abundance and SST is shown in Fig. 2. The aim was to illustrate, for a given decade, how the species is associated with temperature across a wide geographical, and therefore temperature, range. Taking *C. helgolandicus*, we find a very simple pattern. The SST 'response' relationship is approximately linear (no significant quadratic terms) and there is no significant difference in the response across the decades ($P = 0.54$), that is, the common model provides the most appropriate fit to the data. For *C. finmarchicus*, there is a more complicated pattern. First, the relationship is nonlinear, with the greatest response in abundance being found at the lower temperatures that are characteristic of this species. Second, a likelihood ratio test shows a highly significant change in the relationship between the decades ($P = 0.00067$). Might these different response curves across the decades be representative of thermal adaptation? The consistent decline in the slope of the response relationship between the 1960s and 2000s (see Table S3 for regression equations) suggests that the decline in abundance per unit increase in temperature has reduced over time, as might be expected from adaptation. However, this has also been accompanied by a change in the intercept over the decades. This shows that the abundance at an equivalent SST is lower than expected in the later decades (as expected from the changing relationships described in Fig. S2). This later effect clearly dominates the overall population (as shown in Fig. 1) and any evidence for a positive adaptation of the population to temperature is extremely limited.

Discussion

The central finding from our study is that over a large basin-wide scale, for important members of the zooplankton there is limited evidence of thermal adaptation: decreases in the abundance of the cold-water species and increases in the abundance of the warm-water species have been maintained throughout the last 50 years and are strongly linked to SST. These findings help to answer a key ecological issue that also has important socio-economic implications, namely will thermal adaptation by species help mitigate the impacts of climate change? Our findings suggest it will not for these important members of the plankton.

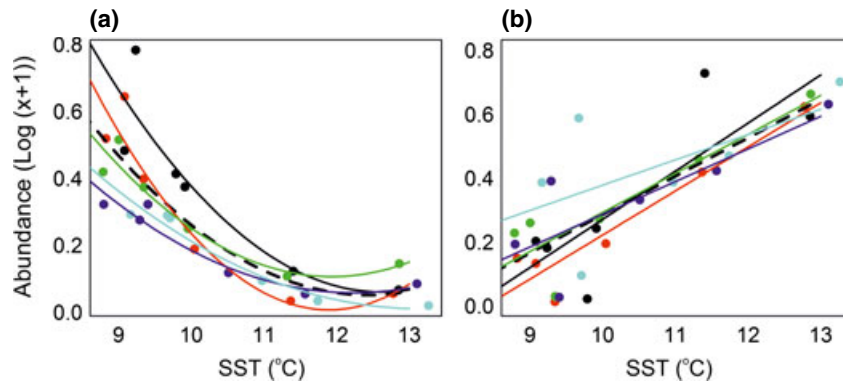


Fig. 2 Decadal interregional temperature response relationships for (a) *C. finmarchicus* and (b) *C. helgolandicus* abundance. The mean values were used from six regions in each decade. *C. finmarchicus* was best fitted with a quadratic function and *C. helgolandicus* with a linear regression. 1960s: solid black circle and solid black lines; 1970s: solid red circles and solid red lines; 1980s: solid green circles and solid green line; 1990s: solid dark blue circles and solid dark blue line; 2000s: solid light blue circles and solid light blue line. Black dashed line is the (a) quadratic or (b) linear regression for all data. The model for decadal changes in the regression coefficients was statistically significant for *C. finmarchicus* only.

Several studies, which examine climate change impacts on species abundance and distribution, have attempted to link biological changes with environmental conditions. However, it is often noted that simple correlations do not necessarily mean causality. Plankton time series are no exception with various environmental drivers being previously linked to plankton abundance including wind speed and direction (Planque & Fromentin, 1996), the NAOI (Fromentin & Planque, 1996) and SST (Beaugrand *et al.*, 2002). In some cases, the correlations with environmental factors have been used to predict future levels of abundance (Helaouet & Beaugrand, 2007). Our results add to the growing body of evidence that cautions against making predictions of future biological changes in this way, especially when available time series are short, since links to environmental correlates can change appreciably. In our analysis, previously strong correlations have weakened as time series have lengthened and the extended 50-year time series shows that SST has emerged with the strongest links to *Calanus* abundance. The importance of SST during the first decades of the time series may have been masked by the fairly limited range of SSTs experienced, but this situation has changed with the extended increase in SST continuing since the 1980s.

In the simplest terms, we might use the strong links between *Calanus* abundance and SST pervading across the last 50 years to predict that future ocean warming will continue to cause range contractions for *C. finmarchicus* and range expansions for *C. helgolandicus*. However, this prediction ignores any potential thermal adaptation by these species. For a cold water species showing thermal adaptation, we predict that abundance at the warmer temperature limits of the species

range will increase over time. However, this was not the case for *C. finmarchicus*. Rather there was little change in abundance at warmer temperatures, but a decrease in abundance at colder temperatures (9–10 °C). This pattern seems to have emerged through a sharp decline in *C. finmarchicus* abundance in the Norwegian Sea that cannot be attributed to SST alone. Some aspects of the life history of *C. finmarchicus* are well known. In particular in the NE Atlantic region, *C. finmarchicus* is known to overwinter in deep water (>500 m) off the shelf as a juvenile stage (copepodite V), surviving on stored lipid (Heath *et al.*, 2004). At the end of the winter individuals ascend to the surface, metamorphose into the adult stage, reproduce and are then dispersed by ocean currents to new areas. In this way, egg production is timed so that the developing next generation is present when maximal food abundance is occurring during the spring plankton bloom (Niehoff *et al.*, 1999). Therefore, advection of individuals by ocean currents (Beare *et al.*, 2002; Reid *et al.*, 2003) and the match–mismatch in the timing of *C. finmarchicus* reproduction in relation to the spring phytoplankton bloom, may both be important in driving the copepods' abundance. Our results suggest that such processes may have contributed to a decline in *C. finmarchicus* abundance that cannot simply be attributed to rising SSTs. This observation also re-iterates the concerns of simple climate envelope modelling that use past environmental niches to predict future levels of abundance of distribution for species (Losos, 2008; Pearman *et al.*, 2008). Such an approach, if based on data from the first few decades of the CPR time series, would have failed to capture the extent of the recent decline in *C. finmarchicus* in the Norwegian Sea.

The lack of thermal adaptation for both *C. finmarchicus* and *C. helgolandicus* is somewhat surprising given recent experimental evidence for adaptation in some other zooplankton. For example, fast adaptation to rising temperature occurred in experimental populations of freshwater planktonic crustaceans subjected to crashes and subsequent growth (Van Doorslaer *et al.*, 2009). However, these experimental studies also highlight the complexity of making extrapolations to natural systems, since thermal adaptation was not seen in more stable populations. Our results highlight the need for further studies on natural systems to complement more controlled experimental manipulations. The observed huge reduction in *C. finmarchicus* abundance may partially reflect a movement to a greater depth. The CPR samples in the upper 20 m of the water column, but recent net sampling has shown that appreciable numbers of *C. finmarchicus* continue to reside at greater depths in the North Sea (Jonasdottir & Koski, 2011), so as well as a northerly contraction of range *C. finmarchicus* may also be shifting its depth distribution. However, the CPR derived levels of abundance for *C. finmarchicus* and *C. helgolandicus* have been strongly linked to changing fisheries recruitment (Beaugrand *et al.*, 2003; Beaugrand & Kirby, 2010), so the implications of our findings for fisheries may be profound. The lack of thermal adaptation in *C. finmarchicus* means that the species range is expected to continue to contract as the NE Atlantic region continues to warm. *C. finmarchicus* is a key prey item for gadoid fish (cod, hake), so continued declines in abundance will likely exacerbate long-term declines in cod and hake stocks in the North Sea and other areas in the southern part of their range. At the same time, the continued increase in abundance of *C. helgolandicus* will likely play a role in the emergence of new fisheries for warm-water species.

Acknowledgements

The CPR survey is supported by a funding consortium comprising: Intergovernmental Oceanographic Commission (IOC), United Nations Industrial Development Organisation (UNIDO), the European Commission and agencies from Canada, Denmark, the Netherlands, the United Kingdom and the United States. The survey depends on the voluntary cooperation of owners, masters and crews of merchant vessels that tow the CPRs on regular routes. We thank CPR survey teams past and present and David Johns for extracting data for us from the CPR database. We thank Steve Worley for supplying and helping us with the ICOADS data set.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Inspection of the Granger causality time series models: ‘Carry-over’ effects.

Fig. S1. North Atlantic CPR data separated into six regions.

Fig. S2. Correlation analysis by the modified Chelton method, measuring the changing significance values of the correlation coefficient for the relationships between the NAOI (solid blue line and closed blue circles), annual SST (solid green line with closed green circles) and annual westerly wind speed (solid red line with closed red circles), for the abundance of (a) *C. finmarchicus* and (b) *C. helgolandicus* for the NE Atlantic region. Correlation was first calculated for 1960–1992. Subsequently, 1 year was added, and at each step a new correlation coefficient calculated until 1960–2010. Black dashed line represents the 5% significance level (due to the use of the modified Chelton method, a guide to significance is given by the average significance level over the three time series: NAOI, SST, westerly wind speed. Note that in all analyses, specific significance levels are used). The sign of the Chelton method coefficient represents the direction of correlation: negative correlation for *C. finmarchicus* and positive correlation for *C. helgolandicus*.

Fig. S3. Correlation analysis by Pearson’s correlation, a 32-year moving window Pearson’s correlation, linear regression coefficient (beta value) and a 32-year moving window of linear regression coefficient (beta value).

Fig. S4. A stationary autoregressive process $Y_{t+1} = c + \phi Y_t + \varepsilon_t$ (where c is a constant, ε_t is white noise, and $|\phi| < 1$).

Table S1. The significance of modified Chelton correlation for *C. finmarchicus* and *C. helgolandicus* against annual Sea Surface Temperature (SST), annual Westerly Wind speed (WW), and the winter NAOI (* $P < 0.05$). The sign of the affect of SST, WW or NAOI on abundance is indicated (+ or –).

Table S2. Granger-causality in the relationships between *C. finmarchicus* and *C. helgolandicus* abundance versus annual SST and annual westerly wind speed (WW) and the winter NAOI. Significant relationships ($P < 0.05$) indicated by *. Lag time scale represents years.

Table S3. Decadal relationship between *C. finmarchicus* and *C. helgolandicus* abundance against SST for both linear and quadratic regression.