

CLIMATE AND RECRUITMENT OF ROCKY SHORE INTERTIDAL INVERTEBRATES IN THE EASTERN NORTH ATLANTIC

BERNARDO R. BROITMAN,^{1,2,3,7} NOVA MIESZKOWSKA,^{4,5} BRIAN HELMUTH,⁴ AND CAROL A. BLANCHETTE⁶

¹National Center for Ecological Analysis and Synthesis, State Street 735, Suite 300, Santa Barbara, California 93101 USA

²Centro de Estudios Avanzados de Zonas Áridas (CEAZA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

³Center for Advances Studies in Ecology and Biodiversity (CASEB), Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile

⁴Department of Biological Sciences, University of South Carolina, Columbia, South Carolina 29208 USA

⁵Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth PL1 2PB United Kingdom

⁶Marine Science Institute, University of California, Santa Barbara, California 93106 USA

Abstract. Studies of the impacts of climate and climate change on biological systems often attempt to correlate ecological responses with basin-scale indices such as the North Atlantic Oscillation (NAO). However, such correlations, while useful for detecting long-term trends, are unable to provide a mechanism linking the physical environment and ecological processes. Here we evaluate the effects of the NAO on recruitment variability of rocky intertidal invertebrates in the North Atlantic examining two possible climate-related pathways. Using a highly conservative test we interpret associations with the NAO integrated over a season (three months) as an indicator of atmospheric effects on newly settled recruits (NAO3), and the effects of the NAO integrated over six months (NAO6) as an indicator of changes in ocean circulation affecting patterns of larval transport. Through an extensive literature survey we found 13 time series, restricted to southwest Ireland and Britain and comprising five species, that could be used for statistical analysis. Significant correlations with NAO3, our proxy for atmospheric effects, were observed in the south-central domain of our study region (southwest Ireland and south England). Significant correlations with NAO6, the proxy for ocean circulation effects, were detected on southwest Ireland. The associations were detected for three (two barnacles and a topshell) at two sites. These results suggest that the NAO can have effects on the recruitment of intertidal invertebrates through different pathways linked to climate and be distributed heterogeneously in space. Based on previous evidence and the sign and geographic location of significant correlations, we suggest that winter NAO effects are likely to occur as a result of effects on the survival of early life stages settling during spring or through changes in phenology. Our results argue that a combination of modeling and synthesis can be used to generate hypotheses regarding the effects of climate on recruitment and aid in the design of field-based tests of explicit ecological mechanisms.

Key words: climate effects; invertebrate; NAO; North East Atlantic; recruitment variability; rocky intertidal.

INTRODUCTION

Studies of the impacts of climate and climate change on biological systems often characterize aspects of climatic variability using basin-scale indices such as the El Niño–Southern Oscillation Index (SOI) or the North Atlantic Oscillation (NAO). These indices are useful as they collapse multiple aspects of the physical environment, including ocean currents and air and water temperature, wave height, salinity, wind, and rainfall into a single parameter, and are thus generalizable “phenomena” rather than definable changes in single environmental variables (Stenseth et al. 2002, Hallett et al. 2004, Zhang et al. 2007). Moreover, these studies have shown that such large-scale indices can serve as

more effective indicators of ecological response than individual weather parameters collected at the scale of the organism (Stenseth 2007). However, while indicative of large-scale processes, correlations between biological responses and indices such as NAO fail to provide mechanistic linkages between changes in environmental parameters and ecological responses of organisms (Hallett et al. 2004, Helmuth et al. 2006b).

Importantly, organisms respond to the immediate characteristics of their habitat, and two organisms living in the same habitat may experience radically different environments (Kearney 2006). For example, a predator and its prey, exposed to precisely the same conditions of weather, may experience very different conditions of body temperature (Porter and Gates 1969). Simply mapping climate, or proxies of climate such as NAO, may therefore not always provide an accurate indicator of how parameters such as physiological stress change

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Corresponding Editor (ad hoc): C. W. Cunningham.

⁷ E-mail: broitman@nceas.ucsb.edu

over long time scales (Hallett et al. 2004) because each organism will “translate” the environmental signal differently (Helmuth et al. 2006b).

The utility of broad-scale indices of climate as predictors of ecological responses to future climatic change, especially on a spatially explicit basis, may therefore be somewhat limited (Helmuth et al. 2006b).

One viable alternative is to hindcast (or forecast) the ecological responses by considering the detailed physiological responses of organisms based on a mechanistic understanding of their interactions with their physical environment (Gilman et al. 2006, Helmuth et al. 2006a). For example, Wethey and Woodin (2008) successfully hindcasted shifts in the range distributions of two ecologically important species of intertidal invertebrates based on a detailed knowledge of their physiological tolerances to temperature combined with historical sea surface temperature data (Wethey and Woodin 2008). The disadvantage of such an approach is that it is time consuming, and requires an advanced knowledge of organismal physiological responses to climate-related environmental parameters such as temperature. Here we explore a hybrid of these two extremes. Specifically, our goal is to better understand the mechanisms underlying correlations between the NAO and ecological responses by separating the atmospheric effects of NAO from the effects of NAO on circulation. While our approach is strictly correlative and post hoc in nature, our goal is to generate hypotheses that can then be further tested under field conditions.

Increased understanding of climate change and associated patterns of environmental variability are essential to assess the likely range of future climate fluctuations and the extent to which they will impact biological systems. Indices of large-scale atmospheric and oceanic activity are potentially useful as a means of synthesizing and transferring physical processes such as air and sea surface temperature into quantitative information such as changes in population abundance and species range shifts. Accordingly, several studies have identified a variety of ecological impacts in North East Atlantic marine ecosystems resulting from atmospheric and oceanographic changes associated with the NAO (reviewed by Stenseth et al. 2002). Specifically, these studies have shown that changes in the strength of the NAO affect marine organisms both via influences on dispersal of adults and propagules and via direct physiological effects through temperature and salinity. As a result, shifts in phase and strength of the NAO have been linked to alterations in primary and secondary production, abundance, seasonal migration, and community structure in a number of pelagic taxa including plankton and jellyfish, and benthic invertebrates from soft-bottom habitats (Taylor and Stephens 1980, Fromentin and Planque 1996, Tunberg and Nelson 1998, Belgrano et al. 1999, Nordberg et al. 2000, Simms et al. 2001, Beaugrand et al. 2002).

The NAO has also been shown to be a strong driver of recruitment variability, with recruitment strength showing strong positive correlations with the NAO index for several species of commercial fish (Alheit and Hagen 1997, Planque and Fredou 1999, Ottersen and Loeng 2000, Dippner and Ottersen 2001, MacKenzie and Köster 2004). Changes in the phase and strength of the NAO have also been shown to alter the degree and direction of dispersal of fish larvae to the shores in the North East Atlantic due to alterations in the strength and direction of winds and surface ocean currents, and the sea surface temperature (SST) to which both adults and larvae are exposed. Many of these studies, however, have found that the NAO often only accounts for a small proportion of the variance in the biological phenomenon being observed. Thus, a mechanistic understanding of the role of the various components described by this index is often difficult to tease apart. For example, determining the impacts of the NAO on fish recruitment is hindered by the difficulties in accurately quantifying the standing stock biomass and the annual cohort strength of open ocean pelagic fish stocks that have been shown to geographically shift in response to fluctuations in climate and hydrographic events (Alheit and Hagen 1997). Here, we examine the influence the effects of the NAO on the recruitment of noncommercially harvested invertebrate species in the North Atlantic Basin, and attempt to separately examine the influence of atmospheric components of the NAO (e.g., onshore post-settlement mortality due to aerial exposure at low tide) from those of effects related to oceanic circulation (i.e., larval dispersal).

The North Atlantic Oscillation (NAO)

The NAO measures the meridional (north–south) oscillation in atmospheric mass arising from variations in atmospheric pressure conditions during the northern hemisphere winter. The index represents the pressure difference between the subtropical high pressure center above the Azores and the polar low pressure centre above Iceland. During positive NAO conditions the axis of maximum atmospheric moisture transport is aligned to the north-east, and strong westerly winds traverse the ocean on a more northerly track (Walker and Bliss 1932, Hurrell 1995). These winds drive warm, moist air onto the European continent, resulting in a northeastward shift in the Atlantic storm activity, mild and moist winter conditions in Scandinavia and northern Europe, and colder, dryer conditions in the Mediterranean and southern Europe (Van Loon and Rogers 1978, Hurrell and Van Loon 1997). A significant decrease in atmospheric moisture transport occurs simultaneously over southern Europe, the Mediterranean, and North Africa.

When the NAO flips to a negative phase, westerly winds weaken and follow a more southerly track, drawing cold air onto Britain and northern Europe (Pingree 2002). Southern Europe and the Mediterranean experience warmer, wetter winters than during a positive

NAO (Hurrell and Van Loon 1997). Shifting wind stress patterns also drive oceanic circulation and control sea temperature patterns via heat advection (Hurrell and Van Loon 1997, Marshall et al. 2001, Pingree 2002, 2005, Trigo et al. 2002). Hydrodynamic responses to changes in phase of the NAO occur with approximately 6–12-month time lags (Marshall et al. 2001, Pingree 2002). These changes are driven by the different atmospheric flow patterns associated with the different NAO phases and affect the strength of two of the main oceanic currents in the North East Atlantic: the North Atlantic Current (NAC), which is a major northern branch of the North Atlantic Drift Current located between 48–53° N, and the Azores Current (AC) which is centered about 34–35° N (Hurrell and Dickson 2004). Many coastal currents derived from NAO-induced sea level anomalies are small in magnitude, but the effects will apply over a large region, resulting in coherent and significant changes in water circulation over large regions of coastal and open ocean areas (Pingree 2002).

Rocky intertidal ecosystems

In contrast to fish, non-commercially harvested intertidal organisms provide an opportunity to assess the overall impacts of changes in the climatic regime on recruitment variability, independent of the confounding effects of fishing on demography. Rocky shore communities have been extensively studied in the Atlantic (Orton 1920, Southward and Crisp 1954, Lewis 1964, Connell 1972, Menge 1976, Bertness et al. 1992, Southward et al. 1995, Leonard 2000) and intertidal studies have long served as major contributors to the development of ecological theory (Paine 1994). Most sessile intertidal invertebrates are from lower trophic levels, and thus are expected to respond more quickly to alterations in local conditions than species at higher trophic levels; they often show the first response in a cascade of effects up the food chain to tertiary and apex predators that all may display a time lag in their response (Jenouvrier et al. 2003). Despite the suitability of the rocky intertidal ecosystem for climate studies and their occurrence along the entire length of the North East Atlantic coastline, very few studies have attempted to mechanistically link the ecological dynamics of these habitats to large-scale environmental variability (Mieszowska et al. 2006; N. Mieszowska, M. A. Kendall, J. R. Lewis, R. Leaper, A. J. Southward, P. Williamson, and S. J. Hawkins, *unpublished manuscript*).

Effects of NAO on intertidal invertebrates

The existence of a well-characterized physical scenario of alternating environmental conditions such as the NAO offers the opportunity to gain some mechanistic understanding of the effects of large-scale climatic variability on population dynamics. The success of marine species with complex life histories, where the reproductive success of the adult populations may be decoupled from the density of new recruits to the

population, is affected by both the supply of new individuals to that population, as well as by the survival of those recruits (Underwood and Denley 1984, Lewin 1986, Roughgarden et al. 1988). The recruitment dynamics of rocky shore intertidal invertebrates can be directly influenced by climate through atmospheric and/or oceanographic effects on the survival and transport of early life stages (Gaylord and Gaines 2000, Jenkins 2005). Moreover, these physical transport processes are inextricably linked to biological processes through their effects on larval development, the timing of settlement and post-settlement mortality (Shanks 1995, Jarrett 2003).

Recruitment variability plays a dominant role in determining patterns of population density and community structure over a broad range of spatial and temporal scales (Connell 1961, Lewis 1976, Gaines and Roughgarden 1985, Van Der Meer et al. 2001, Hughes et al. 2002, Svensson et al. 2006). For example, survival rates during the first year of life have been shown to determine the year class strength in marine invertebrates (Kinne 1970, Bowman 1977, Caffey 1985) and vertebrates (Hjort 1919, Limburg et al. 1999), and have also been seen to affect the fecundity, growth, and adult size of cohorts upon reaching maturity (Ottersen and Loeng 2000, Lindstroem and Kokko 2002). The survival and physiological performance of newly settled recruits is also strongly affected by atmospheric processes that affect the aerial body temperatures of intertidal invertebrates during exposure at low tide (reviewed in Helmuth et al. 2006b). The variability in both atmospheric and oceanic conditions described by the NAO thus presents an excellent opportunity to examine the effects of the changing physical environment on the recruitment of intertidal invertebrates. We therefore define atmospheric processes as those that are most likely to affect the survival of newly settled recruits during aerial exposure at low tide, and oceanic processes as those that are most likely to affect the survival and dispersal of invertebrate larvae and gametes in the water column.

Importantly, the issue at hand is not whether or not these varying mechanisms (atmospheric and oceanographic) affect the survival of larvae; many previous studies have examined these interactions. The question that we ask is, can these factors, aggregated under the NAO index, be sufficiently decoupled so that their effects can be independently examined? Here we use a combined array of ecological knowledge and published long-term studies on the rocky shores of the North Atlantic to evaluate the potential for large-scale climatic effects on recruitment variability across a variety of intertidal invertebrates. We conducted an extensive evaluation of the available peer-reviewed literature and compiled time series of rocky shore invertebrate recruitment. We attempted to unravel a signature of the NAO on larval recruitment using two different windows of temporal integration representing distinct

environmental pathways. We interpret statistical associations with the NAO integrated over a short temporal window as indicative of atmospheric (physiological effects during aerial exposure) effects on newly settled recruits. On the other hand, associations with NAO integrated over a longer temporal window are taken as an indicator of changes in ocean circulation affecting patterns of larval transport. Based on our results and previous evidence, we highlight some of the potential pathways through which climate may exert an effect on benthic recruitment across the region.

METHODS

Study species

The rocky shore fauna of the North Atlantic region comprise a mixture of warm temperate and cold boreal species. Many rocky intertidal invertebrates have temperate and cold water congeners, whose distributions overlap for a large section of their geographical distributions in Europe and North Africa (Crisp and Southward 1958). *Chthamalus montagui* is a temperate water barnacle with southern distributional limits in Africa and northern limits in north Scotland (Crisp and Southward 1958, Mieszkowska et al. 2005). The species contains brooding embryos from spring through to autumn (Crisp and Southward 1958, Burrows 1992) with numbers peaking between June and August when water temperatures reach 15–16°C (Crisp 1950). A latitudinal cline in the onset of breeding and subsequent spawning of larvae has been reported in Europe, ranging from February in the Mediterranean to June in southwest Scotland (Burrows 1992). Planktonic larvae remain in the water column for approximately six weeks before settling on shores on European seaboard of the North Atlantic during the summer (O’Riordan et al. 2004). The Australasian temperate water barnacle *Elminius modestus* is invasive to Europe, having been first introduced to Britain via ballast water in the 1940s (Crisp 1958). *E. modestus* breeds continually throughout the year in northern Europe, and the planktonic larval phase is approximately a month in duration, and settlement is also observed year round on European shores (Crisp and Davies 1955).

Balanus crenatus and *Semibalanus balanoides* are cold water species of barnacles with distributions extending from the Arctic south to the coast of France (Crisp and Southward 1958). In contrast to the barnacle species described above, both *Balanus* are obligate, cross-fertilizing hermaphrodites that reproduce during late autumn/early winter in the northeast Atlantic (Barnes 1957, Crisp and Clegg 1960, Barnes 1989). Larvae are brooded in the mantle cavity over the winter and released in spring. While the spawning period of *S. balanoides* is restricted to early spring, larvae of *B. crenatus* are released between February and September, with two peaks observed in spring and summer to coincide with the phytoplankton blooms (Rainbow 1984).

Gibbula umbilicalis is a temperate water topshell that occurs along the North Atlantic coastline from Morocco to Britain (Crisp and Southward 1958, Kendall and Lewis 1986). The northern range edge of *G. umbilicalis* occurs on the northeast coast of Scotland (Kendall and Lewis 1986, Mieszkowska et al. 2005, 2006). It is a broadcast spawner (Williams 1964), with protracted spawning periods recorded towards the southern edge of the range. In contrast, short, midsummer spawning periods have been recorded towards the northern limits of distribution (Kendall and Lewis 1986) but the existence of a latitudinal gradient in the reproductive cycle has not been established (N. Mieszkowska, unpublished data).

Statistical analyses

The rocky shore invertebrate recruitment time series we collected from the literature had several shortcomings. Mainly, the time series were not continuous, of different lengths, and sometimes collected over different periods. In order to overcome some of these limitations, we eliminated time series with fewer than five data points (Petriatis 1991), those that lasted for only a year (O’Riordan et al. 2004), and those collected at resolutions higher than monthly, such as single-season high-frequency monitoring, which were usually never carried out for longer than two years (Bertness et al. 1996, Leonard 2000). These criteria allowed us to retain time series that spanned more than three years (Table 1) and examine the effects of environmental variability through correlations with the NAO. We obtained the monthly time series of the NAO from 1950 to 2005 from the Climate Prediction Center of the U.S. National Oceanographic and Atmospheric Administration website (NOAA; data available online).⁸

We examined the correlations between invertebrate recruitment variability and the monthly NAO index integrated over two time scales relevant to changes in atmospheric and oceanic circulations respectively. NAO variability over the short term (seasonal) was represented by a three-month running mean of the monthly NAO signal (NAO3). NAO variability over longer temporal scales (semiannual) was obtained through a six-month running mean filter (NAO6). Correlations between recruitment and NAO3 are intended to measure the effects of atmospheric processes on recruitment variability while correlations with NAO6 measure the effects of oceanographic processes.

Correlations between time series were carried out comparing the magnitude of recruitment versus the NAO3 or NAO6 index during the month when recruitment data was collected (see Table 1 for details). However, calculating a correlation between two time series sharing a signal (e.g., a seasonal cycle) may generate a spurious pattern of correlation, thus increas-

⁸ (<http://www.cpc.noaa.gov/>)

TABLE 1. Summary of surveys.

Location	Latitude (N)	Longitude (W)	Site name	Species sampled	Study period	Collection window	<i>N</i>	Source
Northern Scotland	58°33'36"	03°47'24"	Fresgoe	<i>Gibbula umbilicalis</i>	1977–1985, 2002–2004	spring	12	1, 2
Northern Scotland	58°32'24"	04°18'00"	Skerray	<i>Gibbula umbilicalis</i>	1977–1985, 2002–2004	spring	11	1, 2
Northern Scotland	58°13'12"	05°18'00"	Clashnessie	<i>Gibbula umbilicalis</i>	1981–1985, 2002–2004	spring	7	1, 2
Irish Sea	54°09'36"	04°45'00"	Isle of Man	<i>Semibalanus balanoides</i>	1977–1981, 1992–1998	March–June	11	3
Wales	52°24'36"	04°05'24"	Aberystwyth	<i>Chthamalus montagui</i>	1979–1985	fall	7	4
Wales	52°38'24"	04°15'36"	Aberaeron	<i>Gibbula umbilicalis</i>	1981–1985, 2002–2004	spring	7	1, 2
Southwest Ireland	51°30'00"	09°18'36"	Whirlpool	<i>Balanus crenatus</i>	2000–2003	every three months	34	4
Southwest Ireland	51°30'36"	09°18'36"	Labrha	<i>Balanus crenatus</i>	2000–2003	every three months	34	4
Southwest Ireland	51°30'36"	09°18'36"	Whirlpool	<i>Elminius modestus</i>	2000–2003	every three months	34	4
Southwest Ireland	51°30'36"	09°18'36"	Labrha	<i>Elminius modestus</i>	2000–2003	every three months	34	4
South England	50°46'48"	04°34'12"	Widemouth	<i>Gibbula umbilicalis</i>	1978–1984, 2001–2004	spring	9	1, 2
South England	50°42'36"	02°57'00"	Lyme Regis	<i>Gibbula umbilicalis</i>	1978–1984, 2002–2004	spring	10	1, 2
South England	50°37'48"	02°22'48"	Osmington Mills	<i>Gibbula umbilicalis</i>	1978–1984, 2002–2004	spring	11	1, 2

Note: *N* is the number of observations.

Sources: 1, Kendall and Lewis (1986); 2, N. Mieszkowska, M. A. Kendall, J. R. Lewis, R. Leaper, A. J. Southward, P. Williamson, and S. J. Hawkins (*unpublished manuscript*); 3, Svensson et al. (2005); 4, Kendall and Bowman (1987); 5, Watson et al. (2005).

ing the probability of a type II error (Legendre and Legendre 1998). Preliminary analyses showed that individual recruitment time series showed no significant autocorrelation (results not shown). The use of Kendall's tau (r_{τ}) avoids the effects of autocorrelation as it is a nonparametric estimator of concordance. To reduce the probability of Type II error, we used Monte Carlo resampling and bootstrapped the calculation of r_{τ} 10 000 times for each site. As a highly conservative test of significance of the association between the time series we used the resulting 95% confidence interval of the correlations as a two-tailed hypothesis test that correlations between NAO and recruitment rates were significantly different from zero (Manly 1997, Martinez and Martinez 2002). Prior to analysis, we removed first-order autocorrelation from the NAO3 and NAO6 time series through differencing (Helmuth et al. 2006a).

RESULTS

We were able to locate a large number of studies addressing questions of recruitment variability on the eastern and western shores of the North Atlantic. However, a total of only five studies met the data quality criteria outlined above. In particular, we were not able to locate any long-term studies on the Western Atlantic rocky shores, and to our knowledge no long-term monitoring programs addressing the recruitment of rocky shores invertebrates are currently in place on the Eastern North American coastline. All the studies

available to us were carried out on the shores of southwest Ireland, Scotland, Wales, and England between May 1977 and September 2004, and comprised the six species discussed in the *Methods* section. From these studies, we were able to select a total of 13 recruitment time series that retained for statistical analysis. The mean number of sampling events comprised by these larval recruitment time series was 17 and they ranged between a total of seven and 34 sampling events. The mean duration of the time series was approximately 16 years with the longest study spanning 27 years and the shortest ones three years (Table 1).

We found few significant correlations, four out of 26, between recruitment time series and NAO3 and NAO6. Significant correlations with NAO3, our proxy for atmospheric effects, were located in the central-south domain of our study region, on southwest Ireland and south England. We did not observe significant correlations for any species along the coast of Scotland or Wales. Two significant positive associations were observed between NAO3 and recruitment. One was between recruitment of the temperate barnacle *E. modestus* at Whirlpool, in southwest Ireland. The other positive correlation between NAO3 and recruitment was for the temperate gastropod *G. umbilicalis* at Lyme Regis, in south England (Table 2A). Correlations with NAO6 and recruitment were only observed at Whirlpool, in southwest Ireland. Recruitment of *E. modestus*

TABLE 2. Locations, sites, and species with significant Kendall's tau (r_τ) correlations between recruitment time series and (A) a three-month running mean of the North Atlantic Oscillation (NAO3) and (B) a six-month running mean of the North Atlantic Oscillation (NAO6).

Location	Site	Species	r_τ
A) NAO3			
Southwest Ireland	Whirlpool	<i>Elminius modestus</i>	0.247
South England	Lyme Regis	<i>Gibbula umbilicalis</i>	0.429
B) NAO6			
Southwest Ireland	Whirlpool	<i>Elminius modestus</i>	0.186
Southwest Ireland	Whirlpool	<i>Balanus crenatus</i>	-0.251

Note: The r_τ values presented correspond to the 50th percentile of the 5000 bootstrapped estimations of the association between the differenced NAO indices and observed recruitment from the literature.

was positively correlated to NAO6, while *B. crenatus* was negatively correlated (Table 2B).

DISCUSSION

The results presented above suggest that coherent responses to climate may be detected across several species over large spatial scales. However, the result that significant relationships were only detected in four out of 13 time series and for three out five species suggests that either (1) our ability to detect these relationships may be limited given the available information or (2) climate-related factors are distributed heterogeneously in space (Helmuth et al. 2006a; Broitman et al. 2008). Importantly, the post-hoc nature of this analysis highlights the strength of combining large-scale correlative approaches with finer-scale experimental approaches, and we view this method as a means of generating hypotheses which may be tested on a species-by-species and site-by-site basis.

The contrasts between the responses of cold and warm water species to recent climate variability are reminiscent to those observed for continental shelf ecosystems across the North Atlantic (Frank et al. 2007). However, our biological datasets are much more restricted both spatially and temporally, and not all the species represented in the available datasets were represented at all sites, limiting our ability to clearly separate effects for cold and warm water species. Keeping in mind these limitations, we focus on highlighting potential physical and biological pathways that may channel NAO effects on the study species and point out future research directions to improve our ability to assess climate effects on coastal invertebrates across the North Atlantic basin.

The immediate expression of the North Atlantic Oscillation are patterns of atmospheric flow and weather (Trigo et al. 2002, Hurrell and Dickson 2004). Hence, we hypothesized that NAO3, an average of the NAO over periods of three months, provided a proxy of atmospheric conditions. Recruitment of the topshell *G. umbilicalis* and the invasive barnacle *E. modestus*, both warm-water species, were positively associated with NAO3, suggesting that the milder winter atmospheric conditions associated with positive values of the NAO index may impinge favorably on the recruitment of both

species on the south-central region. *G. umbilicalis* was by far the best represented species geographically (seven sites from Scotland to England). However, we observed only one positive significant correlation, at one of the two sites in the English Channel. In this way, neither atmospheric temperature nor ocean circulation patterns seem to be affecting the recruitment of *G. umbilicalis* at the central-northern locations.

Annual collections of *G. umbilicalis* recruits were always carried out in the mid-low shore during spring-summer, so the positive associations with NAO3 are a reflection of the effects of weather conditions during late winter and early spring on each year-0 cohort. The lack of correlation between NAO3 and recruitment at all sites apart from Lyme Regis may be due to the timing of low water during Spring tides, which occurs earlier in the morning in the English Channel than at the other locations, and thus the new recruits will be exposed to the coldest daily winter air temperatures at this site. Osmington Mills, which is also located in the English Channel, did not show a positive correlation like Lyme Regis, despite times of low water Springs being similar. This may be due to the presence of the rare phenomenon of a double high water in this sector of the English Channel which occurs two hours after low water, and is particularly pronounced during spring tides. The young flood stand associated with the double tide may cause the *G. umbilicalis* recruits living in the mid-low shore region at Osmington Mills to have less exposure time to cold aerial temperatures in the early mornings and thus decouple recruitment success with the atmospheric conditions indexed by NAO3.

Our results suggest a phenological response to atmospheric conditions associated to NAO in temperate rocky shore invertebrates. The presence of a phenological shift is supported by observations of earlier onset of gametogenesis in several rocky shore invertebrates (including *G. umbilicalis*) during the warmer spring temperatures observed in several recent years in northern Europe. Spawning events seem to be taking place two months earlier in spring in comparison with the summer spawning event observed in cooler years of the late 1960s and early 1980s (Underwood 1972, Garwood and Kendall 1985, Mieszkowska et al. 2005).

The phenological shift cascades across the complex life history of most marine invertebrates. For topshells in Britain, early spring release of gametes results in veligers settling on the shore earlier in the summer (Garwood and Kendall 1985; M. A. Kendall, *personal communication*; N. Mieszkowska, *personal observation*). Microbial films, which are a key resource for the newly settled larvae, are not at their peak on the shore until late autumn in Britain (Thompson et al. 2005). In this way, the change in phenology associated to an early spawning strategy does not appear to be one of match/mismatch to food resources in either warm or cool conditions. It is more likely that early larval arrival to the shore allows new recruits to feed for a longer period, thus accumulating more metabolic reserves and increasing their body size prior to exposure to extreme cold temperatures once body temperatures drops below a winter threshold (12°C in south England) when feeding stops (N. Mieszkowska, M. A. Kendall, J. R. Lewis, R. Leaper, A. J. Southward, P. Williamson, and S. J. Hawkins, *unpublished manuscript*). The earlier larval recruitment and the accompanying prolonged year-0 stage indicate a phenological shift towards earlier spring reproduction, echoing that recorded for zooplankton in British coastal waters (Edwards and Richardson 2006). Because of its particular geographic location, even the single-site correlation between *G. umbilicalis* recruitment and NAO detected in our study suggests that changes in phenology is a likely mechanism driving recent recorded range extensions in these and other species of intertidal invertebrates (Mieszkowska et al. 2006; N. Mieszkowska, M. A. Kendall, J. R. Lewis, R. Leaper, A. J. Southward, P. Williamson, and S. J. Hawkins, *unpublished manuscript*).

The invasive barnacle *E. modestus* reproduces continuously throughout the spring and summer months of the year, redeveloping as soon as each brood matures (Crisp and Chipperfield 1948, Crisp and Davies 1955, O'Riordan and Murphy 2000). A phenological response does not have very dramatic consequences for species that reproduce continuously. However, milder winter conditions may extend the favorable environmental window for spawning and provide *E. modestus* with a competitive advantage in terms of colonization of empty space during periods of the year when the larvae of native barnacles are not recruiting. Recruitment time series for this species were limited to two sites in a single location in southwest Ireland (Lough Hyne; Watson et al. 2005). In agreement with an NAO signal we observed significant correlations only in the site with strongest exchange with the open ocean (Whirlpool).

The atmospheric asymmetry measured through the NAO index takes several months to develop into an oceanographic pattern (Marshall et al. 2001, Pingree 2002). Hence, correlations between NAO6 and recruitment were intended to examine climate-driven changes in ocean circulation patterns. Similar to its association with NAO3, recruitment of the invasive barnacle *E. modestus* at Whirlpool, southwest Ireland, showed a

significant positive association with NAO6. *E. modestus* therefore appears to be influenced both by atmospheric influences on the survival of newly settled recruits during the first winter and spring due to warmer sea temperatures and aerial body temperatures, and by oceanic currents during the larval dispersal phase. Increased delivery of larvae back from the pelagic oceanic phase to the shore at Whirlpool is likely during NAO positive phase events in opposition to loss of larvae at sea in the Atlantic Ocean when water currents follow a more southerly track during an NAO negative phase event (Hurrell 1995). In contrast, the boreal barnacle *B. crenatus* showed negative correlations at the same location. This finding supports recent observations of a decrease in *B. crenatus* abundance in the region (Southward and Crisp 1954, Mieszkowska et al. 2005, Simkanin et al. 2005) and suggests that the increased onshore flow in the sector associated to the recent intensification of the North Atlantic Drift (Hurrell and Dickson 2004) has a negative demographic effect in these boreal species in the region. Hence, climate-driven changes in ocean circulation may have negative impacts for this species either through reduced larval transport to shore or through other events during the planktonic larval period.

Compelling evidence for the effects of NAO on benthic communities through recruitment variability has only been documented in studies of the soft-bottom communities in the Wadden Sea. The primary cause of temporal variation in the abundance of intertidal and shallow subtidal bivalves in the Wadden Sea is recruitment. This is mediated by winter sea surface temperature (Beukema et al. 1998, 2001, Van Der Meer et al. 2001, Beukema and Dekker 2005) and exhibits a strong negative correlation with the strength and sign of the NAO index (Blenckner and Hillebrand 2002). Strong annual variability and synchronous recruitment success or failure has been recorded in populations located across hundreds of kilometers of seabed (Beukema et al. 2001). This modulation of ecosystem dynamics by NAO-related environmental conditions appears to be driven by two temperature-dependent processes: bottom-up effects on the number of eggs produced by female bivalves and top-down effects via the density of predating shrimps on new recruits (Beukema et al. 1998) demonstrating the role of NAO-related sea temperature as a strong structuring factor in shallow benthic communities. Complex physiological responses or interactions resulting from sea temperature regimes may also occur but are likely to be nonlinear and therefore difficult to categorize (Ottersen et al. 2001).

Given the limited data sets available for rocky shores, the results outlined by our study provide a starting point to disentangle the mechanisms by which large-scale climatic variability affects these communities. The rocky intertidal habitat spans the ocean-atmosphere interface and is subject to perturbation by both environments. Winter freezing conditions experienced during low tide

and sea surface temperature (SST) appear to be primary drivers in the success of intertidal species in the boreal section of the northern hemisphere, due to the timing of reproduction and the arrival of new recruits. The NAO is predominantly a winter phenomenon (Cassou et al. 2004), and the links between NAO and SST continue to affect temperatures into the following spring, when many species enter their reproductive phase and when most of the data used in our analyses was collected. In this way, the winter nature of NAO finds a clear pathway of expression through either phenological changes or survival of the young. A switch to negative NAO during winter would likely favor species of cold water origin, reversing recruitment success rate in warm vs. cold water invertebrates. If the event were of sufficient magnitude, or if the NAO remained in the negative phase for successive winters, the biological impacts may be carried across several consecutive years due to the longevity and life-cycle characteristics of many intertidal species. In contrast, during a switch to positive NAO southern species will show increases in reproductive success and competitive dominance, albeit with occasional and potentially localized perturbations. Some initiatives have already confirmed the differential seasonality among the same invertebrate species across Europe highlighting the potential for differential effects of NAO variability with latitude (O'Riordan et al. 2004). However, linkages to climatic variability can only be examined once large-scale, long-term ecological monitoring programs have been in place for several years (Hughes et al. 2002, Navarrete et al. 2005, Broitman et al. 2008). Our understanding of climate effects on coastal ecosystems will only improve after ecological monitoring programs are sustained in time and networked across ocean basins.

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