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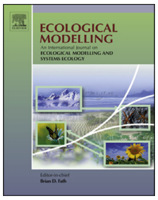

Testing the effects of temporal data resolution on predictions of the effects of climate change on bivalves

Valeria Montalto[a,1], Gianluca Sarà[a,*,1], Paolo Michele Ruti[b,1], Alessandro Dell'Aquila[b,1], Brian Helmuth[c,1]

[a] Dipartimento di Scienze della Terra e del Mare, Università di Palermo, Palermo, Italy
[b] ENEA, Energy and Environment Modeling Unit, Santa Maria di Galeria, Roma, Italy
[c] Department of Marine and Environmental Sciences, Northeastern University, Boston, MA, USA

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ABSTRACT

The spatial–temporal scales on which environmental observations are made can significantly affect our perceptions of ecological patterns in nature. Understanding potential mismatches between environmental data used as inputs to predictive models, and the forecasts of ecological responses that these models generate are particularly difficult when predicting responses to climate change since the assumption of model stationarity in time cannot be tested. In the last four decades, increases in computational capacity (by a factor of a million), and the evolution of new modeling tools, have permitted a corresponding increase in model complexity, in the length of the simulations, and in spatial–temporal resolution. Nevertheless, many predictions of responses such as shifts in range boundaries are often based on coarse spatial and temporal data, for example monthly or yearly averages. Here we model the effects of environmental change on the physiological response of an ecologically and commercially important species of mussel, the fitness of which can have a cascading influence on ecosystem levels. Using a Dynamic Energy Budget (DEB) model integrated with climatic data produced from IPCC-A1B scenarios, we investigated the effect of temporal resolution of physical data on predictions of the growth and reproductive output of the mussel *Mytilus galloprovincialis*. We ran models using five different temporal scales, 6, 4, 3, 2 and 1 h (derived by interpolating between 6 h points), at 5 Italian locations in the Central Mediterranean Sea, for the period ranging from 2006 to 2009. Results from these models were further compared against the results from a DEB model that used hourly environmental data recorded at the five locations as inputs. Model outputs included estimates of life history traits relevant to ecological performance as well as parameters related to Darwinian fitness. Results showed that predictions of maximum theoretical shell length were similar regardless of which source of environmental data was used. However, while the DEB model using 1-h modeled data produced predictions of reproductive output very similar to those obtained using recorded (hourly) environmental data from the same time period, results using coarser resolution modeled data greatly underestimated reproductive output. Thus, the use of modeled weather data can yield predictions similar to those generated from measured data, but only when data are provided at relatively high frequency. Our results suggest that metrics of model skill can diverge significantly when physical outputs of climate models are applied to biological questions, and that the temporal resolution of environmental data can strongly alter predictions of biological responses to environmental change.

1. Introduction

The temporal and spatial scales over which ecological processes operate are thought to be tightly linked to the intrinsic complexity of the system itself (e.g., Mislan and Wethey, 2011; Wernberg et al., 2012). Considerable research has thus focused on the need to study ecological processes under different spatio-temporal scales of observation (Broitman et al., 2008; Wiens, 1996), and has emphasized that spatial heterogeneity in the environment at smaller scales can have cascading impacts on ecological interactions operating at much larger scales, and vice versa (Denny et al., 2006; Menge et al., 2011). Surprisingly, while considerable discussion and debate still exist as to the importance of spatial heterogeneity in physical drivers on ecological processes (e.g. Burrows et al., 2009; Denny et al., 2011; Hallett et al., 2004; Wiens, 1996), there has been less of a focus on the potential role of high frequency temporal variability (but see Benedetti-Cecchi, 2003; Denny et al., 2011; Kearney

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* Corresponding author. Tel.: +39 09123862853; fax: +39 09123862144.
E-mail address: gianluca.sara@unipa.it (G. Sarà).

[1] All authors contributed substantially to revisions.

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et al., 2012). Several studies have argued that the use of monthly or annual means for predictions of niche dimensions and thus distribution limits may miss important drivers that occur over shorter temporal scales, for example when temporal averaging removes rare but extreme lethal events (e.g., Jentsch et al., 2007). Studies have also suggested that temporal averaging can affect our predictions of sublethal responses such as growth and reproduction. For example, Kearney et al. (2012) modeled physiological responses of lizards and showed that predicted growth and reproductive output varied depending on whether environmental inputs were derived from daily or monthly data. Denny et al. (2009) have argued similarly for the importance of considering the temporal patterning of environmental conditions, and especially the return time of physiologically stressful events. A rectification of processes that occur at the scale of organisms, and the long-term, cumulative effects of these organismal responses on communities and ecosystems, remains one of the biggest challenges facing climate change biologists today (Denny and Helmuth, 2009).

The predicted global warming SRE (Special Report Emissions) scenarios provided by the International Panel on Climate Change (most recently, IPCC, 2007) have represented the core of virtually all studies carried out in climate science and global ecology of the last decade, and have been used to forecast significant (and often detrimental) effects of climate change on natural and human-managed ecosystems, and on the ecosystem services that they provide (Hickler et al., 2012; Mumby et al., 2011; Schweiger et al., 2012). A host of studies have been conducted comparing physiological responses under current conditions, against those in which temperatures are increased by ~2–5 °C, and are intended to reflect conditions in a warmer world. However, as emphasized by Stenseth et al. (2002), organisms are affected not by climate (long-term trends in weather), but rather by weather (short-term changes) that is "trained" by climate. That is to say, the most relevant effect of climate on organisms may not lie in low frequency changes in mean conditions, per se, but rather by how patterns of weather are affected, and how these altered conditions in turn affect organisms (Jentsch et al., 2007). Long-term trends in weather (climate) thus ultimately cause effects at ecological scales because of the cumulative effects of weather on individual organisms, but effective prediction requires that we include (or at least eliminate) any potential influences of higher frequency variability that overlies long-term trends. As a result, an emerging number of studies have explored how environmental "signals" are translated into physiological responses by capturing fine-grained differences in the metabolic processes of organisms through an entire life cycle (e.g. Denny et al., 2006; Helmuth et al., 2010). Still, there remains a major conceptual gap between studies conducted at physiological scales and those conducted over large geographic or long temporal scales. Put simply, we do not necessarily know what comprises "signal" and what is simply "noise".

1.1. Thermal physiology

Almost all physiological responses are sensitive to temperature, and the simplest and most frequently used methods for quantifying the relationship between body temperature (BT) and fitness is with a thermal performance curve. A key feature of most performance curves is that they are highly nonlinear. The BT of ectotherms, like most aquatic invertebrates such as bivalves, is driven by the external environment (Lima et al., 2011); in subtidal animals (i.e., always immersed) the body temperature is thus very similar to the temperature of the surrounding water. In some environments water temperature (and hence body temperature) may change slowly, for example over seasonal cycles. Importantly, however, recent studies have shown that such assumptions are not always correct. Nearshore water temperature (and hence body temperature) can exhibit significant hourly fluctuations (several °C) due to the influence of surface heating from solar radiation, upwelling, or internal wave formation (Leichter et al., 2006; Pfister et al., 2007). Variability in BT in terrestrial and intertidal environments during low tide can be much more extreme, with changes of 20 °C occurring over a matter of hours. Subsequently, basing estimates of physiological performance on average conditions is therefore very risky, because the relationship between BT and performance can be highly nonlinear. During the normal course of a day for many organisms, their performance will shift with environmental conditions (move along the thermal performance curve) so that relatively small changes in temperature can lead to large changes in performance. Thus, for example, estimates of physiological responses in an animal with a BT fluctuating between 10 and 20 °C may not be accurately reflected by performance measured at an average temperature of 15 °C. This central thesis suggests that by temporally averaging the drivers of BT, we may be inadvertently biasing the true physiological responses to fluctuating conditions that normally occur in many environments. Quantifying these differences requires an integrative approach that can account not only for rapid changes in physiological performance, but also in the time history of performance.

Whereas the accurate prediction of weather patterns on any particular day at any appreciable time in the future is impossible, climate models can reproduce a coherent chronology (i.e., at 6-h intervals) which represents a possible evolution of the Earth system and thus can effectively overlay "weather" on top of climatic trends. We tested the effect of temporal resolution on correlates of fitness of the Mediterranean blue mussel, *Mytilus galloprovincialis* (Kearney et al., 2011; Sarà et al., 2011). *M. galloprovincialis*, native to the Mediterranean, is listed among the 100 of the World's Worst Invasive Alien Species and is a dominant space occupier and structuring species in many rocky shores. It is also an important aquaculture species (Sarà et al., 2012) and worldwide this genus of mussels is worth approximately USD 0.106 billion in annual harvest (DAFF, 2012). Combining a mechanistic approach based on the Dynamic Energy Budget model (DEB; Kooijman, 2010) and seawater temperatures projected by the PROTHEUS climate coupled model (Artale et al., 2010), specifically developed for the Mediterranean Sea under an A1B scenario (Carillo et al., 2012; Dell'Aquila et al., 2011), we examined how two temporal scales of output from a climatic model – two models with the same accuracy (skill) when based on comparisons of physical environmental data – may result in different expressions of model skill when evaluated using physiological metrics.

2. Materials and methods

Mechanistic (process-based) predictive models such as DEB theory (Kooijman, 2010) represent a potentially valuable and reliable tool for studying physiological and ecological responses in the context of climate change, particularly when coupled with measurements of the physical environment at appropriate spatial and temporal scales (Kearney et al., 2012; Sarà et al., 2011, 2012, 2013a, 2014). A major advantage of these models is their ability to predict not only patterns of mortality, but also sub-lethal responses such as changes in growth, maximum size, and reproductive output. In these models, all aspects of organismal metabolic machinery are generally rate-based, implying that all predictions of organismal processes will be a direct function of physiological rates; i.e. they are not dimensionless (*sensu* Kooijman, 2010). DEB is able to quantify the principal life history traits (e.g. size, time to puberty and number of eggs) as a function of the real amount of energy