



Time and heat for sexual reproduction: comparing the phenology of *Chara hispida* of two populations at different latitudes



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ABSTRACT

Geographical location affects the main ecological factors driving the timing of plants' life events. In addition, studying phenology is the simplest procedure to track current global warming and its effects on the success and survival of different populations of the same species. Little is known about the effect of water temperature and its corresponding accumulated heat on charophytes' phenology. We compared differences in water temperature and sexual reproductive phenology of *Chara hispida* in two ponds of two countries located at different latitudes (Spain and Switzerland) over the same year. We estimated the accumulated heat required to develop from one phenophase to another (unripe/ripe gametangia and oospores). Curve fitting techniques on water temperature showed an advance of 26 days in the Spanish spring onset. All phenological events happened for the first time around 40 days earlier in the Spanish pond, agreeing with the Hopkins' Bioclimatic Law prediction. *C. hispida* sexually reproduced in a daily mean temperature (DMT) range of 10–25 °C and needed 600 growing degree-days (GDD) to ripen gametangia in the Spanish pond. The Swiss population required a higher DMT (15 °C) to begin to reproduce, and ~700 GDD to initiate gametangia ripening. Temperature (as well as radiation) is one of the most important drivers of reproductive phenology, and accumulated heat is a better predictor than DMT for charophyte phenology. In the foreseeable warming scenario, we assume that *C. hispida* sexual events would advance by more than one month in Switzerland and expand at the end of the season, considerably lengthening its reproductive period.

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1. Introduction

Phenology is the study of the seasonal timing of biological events. Organisms develop from one phenophase to another in their life cycle depending on their biology and “internal clock” (Resco et al., 2009). However, authors have also described how the initiation of phenological events is driven predominantly by climatic shifts associated with the change of seasons, rather than by intrinsic controls (Badeck et al., 2004). Unpredictability can affect the success of individuals and populations if it affects the precise timing of events – especially those regarding reproduction, such as flowering or fruiting in plants. Thus, organisms have to respond to environmental factors that are variable from year to year (Ausín et al., 2005). Factors related to light availability (such as photoperiod or irradiance), water availability (such as precipitation or hydrope-

riod) and other climatic factors (such as temperature) act as cues for phenology, as they inform about short-term environmental trends and foreseeable future conditions (Pau et al., 2011). Hence, phenology is considered to be the simplest process which allows us to track the current changing climate and its effects on the ecology of both animal and plant species (Walther et al., 2002).

All the environmental factors that affect phenology vary with the geographical factors in which the organisms are living (Pau et al., 2011), determining the distribution of species (Chuine, 2010). According to Hopkins' Bioclimatic Law, a variation in geographical position – as defined by latitude, longitude and altitude – implies a constant variation in climatic conditions and phenology across temperate areas (Hopkins, 1918). So, with other conditions being equal, there is a progression of spring phenological events from south to north, from west to east and from lower to higher elevation. Hopkins research was focused on the phenology of insects, forest trees, wild shrubs, farm crops and cultivated plants from gardens, all of them being from terrestrial ecosystems. Research based on remote sensing techniques and vegetation indexes (Schwartz,

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1998; Pettorelli et al., 2005) delved deeper into the description of the spring phenology advance in terrestrial plants, the so called “green up”, through latitudinal gradients. For aquatic ecosystems, recent examples of the application of these methods exist (Hestir et al., 2015; Luo et al., 2016), but no information is available concerning the effect of latitude on the reproductive phenology of submerged aquatic plant species or the fulfilment of Hopkins’ Law.

Among environmental factors, light and temperature especially affect phenology by directly influencing biochemical processes and the development rates of organisms (Franklin, 2009). To study the seasonality in environmental factors, curve fitting techniques have been applied, as they allow one to represent the annual pattern on a temporal axis and to characterize some key dates within the year that can be related to biological events. The onset, the maximum or the end of the growing season are some examples of these key dates (Pettorelli et al., 2005) that can be calculated based on temperature dynamic. Other methods can be used to explore phenological events, such as the broadly used growing degree day model, also called the thermal time model (Trudgill et al., 2005). It is based on the accumulation of heat above a base temperature, called the low threshold of temperature. This model assumes that each organism requires a particular heat sum to develop to the next phenophase in its life cycle, so when that required thermal summation is reached, the phenological event is triggered. There are many examples of the application of this model for terrestrial organisms, especially in plants (Zavalloni et al., 2006; Sacks and Kucharik, 2011; Kramer et al., 2012). However, its use for submerged macrophytes is scarce (Spencer et al., 2000; Spencer and Ksander, 2001), particularly for green macroalgae such as charophytes (Rey-Boissezon, 2014; Calero et al., 2015).

Charophytes play key roles in aquatic ecosystems (Schneider et al., 2015). They form dense stands in permanent waterbodies by means of their high capacity for vegetative reproduction. In spite of this, the disappearance of several charophyte species, and the decline of rarer ones, have already been reported for Europe (see, for example, Simons and Nat, 1996; Auderset Joye et al., 2002; Korsch et al., 2008; Auderset Joye and Schwarzer, 2012; Baastrup-Spohr et al., 2013). Reducing the risks to which charophytes are exposed requires a better knowledge of their ecology. Under the current scenario of changing climate (CH 2011, 2011; IPCC, 2014) it is crucial to unravel how charophytes, and their phenological processes, will respond to these perturbations. Even many charophyte species can reproduce vegetatively, higher unpredictability and frequency of droughts are making sexual reproduction more important for charophyte populations. Climate change might affect interactions between temperature and charophyte reproduction, affecting their geographical distributions and threatening the survival of certain species (Auderset Joye and Rey-Boissezon, 2015).

As stated by Marchin et al. (2015), predicting future responses of phenology to climate change in general, and warming in particular, requires a broad perspective and the use of a range of approaches. For instance, differences in temperature between two countries over the same year due to distinct geographical locations could be comparable, with caution, to the increment in temperature that the country located at the higher latitude would experience in the future under the warming scenario. For example, in Switzerland there is a foreseeable increase of up to 4.8 °C in the seasonal mean temperature by the end of the century under a non-intervention scenario (CH2011, 2011). Looking at the seasonal mean air temperature between this country and one located at a lower latitude such as Spain, which is approximately 5.5 °C warmer in spring (in the period 1981–2010; AEMET, 2012; MétéoSuisse, 2015), means that Spain would be a suitable candidate for the comparison of spring phenology. Therefore, in this study we compared the temperature dynamics and the reproductive phenology of the same species during 2014 in two ponds located in Spain and Switzerland. We chose

the submerged macrophyte *Chara hispida*, a European broadly distributed charophyte which lives in both freshwater and brackish water, with a degree of threat rated as vulnerable in Switzerland (Auderset Joye and Schwarzer, 2012). The aim of the study was to answer the following questions: (i) does *C. hispida* follow Hopkins’ Bioclimatic Law? (ii) does the length of the *C. hispida* reproductive season change with the geographical location? and (iii) does the heat sum needed to develop from one phenophase to the next one within a life cycle depend on the geographical position? Summarizing, we tried to understand how geographical factors, through an important climate factor such as temperature, affect the reproductive phenology of the same particular aquatic species.

2. Methods

2.1. Study sites

The two ponds under study were located in two countries within the European continent, differing in their latitude, longitude and altitude (Fig. 1). The *Llacuna Nova del Canyar* (LNC hereafter) is an oligohaline shallow pond created in 2007 within the *Albufera de València* Natural Park (Valencia, Spain) as part of the restoration of a sea-shore dune front. During 2014, scattered meadows of submerged macrophytes covered the sandy bottom, dominated by dense beds of *C. hispida* (Calero et al., 2015).

The *Étang Robert Hainard* (HAI hereafter) is a freshwater pond created in 1991 within the *Moulin de Vert* Nature Reserve (Geneva, Switzerland) in a former meander of the *Rhône* river that disappeared when the river was channelized in 1940. In 2014, charophytes dominated the macrophytes community and, although the pond was covered by ice during part of the winter, *C. hispida* grew perennially in permanent shallower and deeper waters.

2.2. In situ temperature recording

Several Onset HOBO® probes with data loggers (Onset Computer Corporation, Bourne, MA, USA) were set up within the ponds to hourly record the air and water temperatures. All underwater sensors were fixed to the bottom of the pond so that their depth relative to the surface changed with the water level. For this study, however, we defined the depth of each probe related to the water surface –by using the average water level in each case– to understand the phenology of the charophytes sampled at those same depths in other areas of the pond.

Two underwater temperature sensors were located within LNC at different areas with permanent water. One of the probes was located close to the shore of the pond, at a depth of 15 cm in an area 30 cm deep (LNC–15 cm hereafter), where charophytes were growing at the base of emergent vegetation. Another one was placed in open waters, at a depth of 30 cm in an area which is 120 cm deep (LNC–30 cm hereafter). By contrast, in HAI, four underwater sensors were placed at different depths in the same vertical line in an area 400 cm deep (HAI–50 cm, HAI–150 cm, HAI–250 cm, HAI–350 cm hereafter, respectively). See their location within the pond in Fig. 1.

2.3. Calculations and statistics related to temperature data

To describe and compare both studied ponds, we calculated the daily mean temperature (DMT). DMT data from each location and depth were studied by curve fitting techniques to characterize the beginning of spring and autumn in order to relate them with biological events. Scaled data were fitted to two different bell-shaped functions for subsequent model selection (Johnson and Omland, 2004): the Fourier model of 2 terms (Los, 1998) and the Weibull model of 6 parameters (Rolinski et al., 2007). The goodness of fit

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