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Germination characteristics of *Zannichellia palustris* from a northern California spring-fed river

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ABSTRACT

The germination characteristics of *Zannichellia palustris* seeds collected from the spring-fed Fall River of northern California were investigated as affected by temperature, darkness, photoperiod, and light intensity. Darkness significantly inhibited germination; however, once stimulatory light levels were reached, germination time and the fraction of seeds that germinated were neither affected by photoperiod nor light intensity. The effects of temperature were assessed across a range of constant values from 4.2 to 40.8 °C. Seeds germinated at all temperatures except 40.8 °C, while the maximum fraction of seeds that germinated was observed at 24.4 and 29.5 °C, with 69 ± 5 and 73 ± 3% total germination, respectively. Germination times were also fastest at 24.4 and 29.5 °C, where median germination was 9 d. The cumulative spread in germination over time was determined to be log-normally distributed, and was best described by a probit function for both individual temperatures and thermal units derived from linear regressions of subpopulations. These results, which deviate from those reported for *Z. palustris* in other parts of the world, suggest that *Z. palustris* may be able to adapt to local conditions, such as cold spring-fed waters as found in the Fall River of northern California.

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1. Introduction

Submersed macrophytes are critical to the structure and function of many aquatic ecosystems, especially lotic systems (White and Hendricks, 2000). Besides being primary producers, aquatic macrophytes provide structure and substrates for other primary producers (epiphytes), slow water flow rates, enhance nutrient cycling, and provide habitat and food for a range of aquatic organisms within aquatic food webs (Hershey et al., 2011). These interactions, especially as they relate to biotic productivity, are often proportional to the biomass and productivity of the overall macrophyte community (Carpenter and Lodge, 1986). *Zannichellia palustris* (horned pondweed), a globally distributed submersed macrophyte (van Vierssen, 1982a; Greenwood and DuBowy, 2005), is the most abundant native macrophyte in the Fall River (Spencer and Ksander, 1998; USDA and NRCS, 2013), a spring-fed northern California river known for its wild trout fishery. *Z. palustris* and other native macrophytes are vital to the ecological health of the Fall River (see http://caltrout.org/2011/08/caltrout-beginning-restoration-projects-on-hat-creek-fall-river/), which has been threatened by invasions of exotic weeds, such as *Myriophyllum spicatum* (Eurasian watermilfoil) (Spencer and Carruthers, 2012). In comparison to *Z. palustris*, *M. spicatum* has been documented to change habitat structure such that it slows water flow, decreases oxygenation, increases sedimentation rates, and affects other physical and biological factors that alter the composition and productivity of dependent food webs (Madsen, 1998; Eiswerth et al., 2000). The importance of sustaining a dense native plant population has been documented by Capers et al. (2007), who reported that invasive plant occurrence is negatively correlated with native plant density in freshwater lakes in the northeastern United States. Since *Z. palustris* is primarily an annual plant that regenerates each season from newly produced seeds and the seed-bank (van Vierssen, 1982b), it is important for conservation and restoration efforts to understand its seed production and germination dynamics. Such knowledge can help waterway managers predict germination and establishment times, particularly in efforts to enhance *Z. palustris* in waterways threatened by invasions of exotic macrophytes.

Previous studies on the germination of *Z. palustris* seeds have produced some understanding of the germination process as affected by light, temperature, salinity, and low-temperature seed

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storage (van Vierssen, 1982a; Lombardi et al., 1996; Greenwood and DuBowy, 2005), but not over the same range of conditions present in the Fall River. Spencer and Ksander (1998, 1999, 2002) have documented the importance of *Z. palustris* in the Fall River, assessed the effect of sedimentation and burial depth on both the rate and fraction of germination in the waterway, and have assessed nutrient limitations of growth in the Fall River. Further research, however, was needed to assess the germination patterns and dynamics of *Z. palustris* seeds (produced between June and December in the Fall River [unpublished data]) in relation to both measured and controlled environmental conditions, particularly light and temperature.

The presence of light has been observed as a requirement for *Z. palustris* seed germination, especially in seeds that have not been exposed to an extended cold stratification period (van Vierssen, 1982a; Lombardi et al., 1996; Greenwood and DuBowy, 2005). However, both light intensity and photoperiod have not been assessed in regards to *Z. palustris* seed germination. These variables are hypothesized to be important as they change both through different seasons and with increasing water depths. Temperature-dependent germination of *Z. palustris* seeds has been investigated in further detail (van Vierssen, 1982a; Lombardi et al., 1996; Acosta et al., 1998; Greenwood and DuBowy, 2005), however not over the primary range of water temperatures that are present in the Fall River. Furthermore, differences in optimal germination temperatures have been reported for *Z. palustris* populations distributed around the world, indicative of an adaptation to local environmental conditions (Lombardi et al., 1996).

The objectives of the work presented here are to evaluate the effects of light and temperature on the germination of *Z. palustris* from northern California's Fall River, and how germination responses may differ from populations in Europe, Australia, and South America. The temperature and light range under which seeds germinated and how germination totals and rates changed are investigated as applicable to the Fall River. Germination is evaluated by investigating the effects of photoperiod, light intensity, and temperature, which vary temporally and spatially in the river. The cumulative germination process, hypothesized to be primarily driven by temperature in non-dormant seeds, as described in regards to the germination of *Z. palustris* (van Vierssen, 1982a; Lombardi et al., 1996; Greenwood and DuBowy, 2005) and other plant species (Bewley and Black, 1982; Garcia-Huidobro et al., 1982; Steinmaus et al., 2000), is further investigated with the objective of creating a model for predicting germination in the field.

2. Materials and methods

2.1. The study area

The Fall River is primarily a cold water spring-fed river in the northeastern part of Shasta County, California (41°00′17″N; 121°26′18″W). A series of 71 sample locations have been established on the Fall River, each approximately 500 m apart, along this 35.5 km waterway. All studies were conducted in and among these sample sites where a variety of water quality data, such as water temperature (Fig. 1), nutrient levels, and light attenuation as a function of depth (Fig. 2) were monitored. A further description of the Fall River study site is provided in Spencer and Carruthers (2012).

2.2. Germination tests

Mature *Z. palustris* plants, from which newly produced seeds were harvested, were collected from the Fall River on September 21, 2012 and November 8, 2012 between experimental sample site 42 and the Island Road Bridge crossing the Fall River (site 45). Up-rooted plants were then sealed into 2 l plastic containers filled with river-water. These containers were placed in portable coolers containing ice packs for transport to our primary laboratory in Albany, CA. Plants were temporarily stored in Percival Intellus Environmental Controller growth chambers (Percival Scientific Inc., Perry, IA) at 8 °C and in total darkness until all seeds could be harvested and sorted into full experimental sets. A portion of the seeds collected in November was dry-stored for 90 d at 20 °C and in total darkness for use in the photoperiod and differential light intensity experiments which could not be conducted at the time of seed collection.

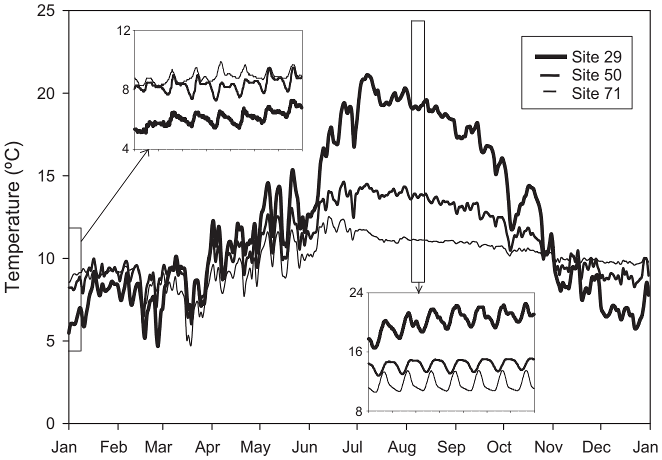

Fig. 1. Mean daily water temperatures from January to December 2011 at three sites in the Fall River, California. Site 29 is roughly the most downstream location where *Z. palustris* is found, site 71 is the most upstream where *Z. palustris* is found, and site 50 is in the middle of the *Z. palustris* habitat in the river. The two insets display measurements recorded at 30 min intervals and show diurnal fluctuations for the three river locations for the first week of January and August.

Seeds were randomly sorted into 100 mm diameter Petri dishes filled with de-ionized water for germination assessment. All experimental seeds were incubated under experimental conditions in temperature and light controlled Percival Intellus Environmental

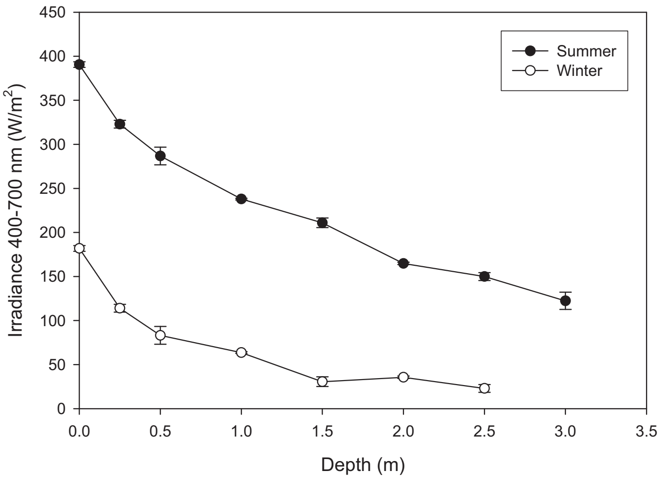

Fig. 2. Mean irradiance in the PAR range (400–700 nm) as a function of depth, as measured on January 16 and August 2, 2013 at approximately 12:00 PM. Measurements were taken from the Spring Creek Bridge near site 57 in the Fall River. Error bars represent the standard error of the mean as determined by three measurements at each depth. Observed values are roughly representative of the maximum light levels available to *Z. palustris* at different depths in the Fall River during winter and summer months. Bear in mind, however, that germinating seeds are typically in shaded canopies or lightly covered by sediments, reducing open water light levels to lesser values.

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