Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Phenotypic plasticity and differentiation in an invasive freshwater microalga

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ARTICLE INFO

Article history: Received 26 June 2014 Received in revised form 4 November 2014 Accepted 10 November 2014 Available online 9 December 2014

Keywords: Gonyostomum semen Growth rate Phenotypic differentiation Plasticity pH Raphidophyte

ABSTRACT

Recent studies show that both marine and limnic microalgal species often consist of several genetically distinct populations. This is also valid for the nuisance freshwater algae Gonyostomum semen, which originates from acidic, brown water swamp lakes, but can nowadays also be found in clearer lakes with close to neutral pH. We hypothesized that the observed genetic differentiation among G. semen lake populations, reported in earlier studies, is connected to adaptation to local environmental conditions. In the present study we performed controlled laboratory experiments to test whether 12 strains originating from five lakes varied in their response to five to six different pHs, light intensities and DOC concentrations. Overall, growth $(0.01-0.37 \text{ dav}^{-1})$ was observed over a wide range of light intensities and pHs, demonstrating high potential for photoacclimation and extensive plasticity of individual strains. Moreover, we found similar growth rates and consistent growth optima for specific pHs by strains from the same lake, suggesting genetic differentiation of populations into distinct phenotypes. However, observed strain specific preferences did not always reflect environmental conditions in the lakes of origin and provided limited evidence for the hypothesized local adaptation. Instead, the observed phenotypic differentiation may indicate resilient effects of founder events. We suggest that the wide phenotypic plasticity in this species enables it to thrive in fluctuating and variable environments, and may play a role in its ability to colonize new habitats.

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1. Introduction

Despite being widespread, many microalgal species are differentiated into genetically distinct populations. In fact, some widely distributed species contain both cosmopolitan and endemic clades at the same time (Godhe et al., 2006; Rynearson et al., 2009; Watts et al., 2011). Genetically diverged populations of harmful algal bloom (HAB) species have been reported in many studies of the toxic dinoflagellate genus *Alexandrium* (Casabianca et al., 2012; Nagai et al., 2007; Tahvanainen et al., 2012). Also, several well-differentiated populations of the marine, red-tide forming raphidophyte *Chattonella marina* were recently described by Demura et al. (2014). Studying the population structure of HAB species is especially important, as high genetic diversity challenges

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¹ Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA. predictions of dispersal and response to environmental changes. Cryptic genetic diversity, expressed in different phenotypes, may allow HAB species to invade new habitats or thrive with global change (Kremp et al., 2012; Litchman, 2010), as they can tolerate a wide range of environmental conditions.

Although high intraspecific genetic diversity in microalgae has been frequently confirmed, the mechanisms behind the divergence is largely unknown (Figuerola and Green, 2002). Genetic differentiation may be caused by limited dispersal due to geological barriers or geographic distance (Papke and Ward, 2004). On the other hand, successful establishment in new habitats might be restricted by biological barriers like founder effects or local adaptation (Foissner, 2008; Weisse, 2008). The monopolization hypothesis, which was established for zooplankton, argues that large genetic differentiation between well-connected habitats can be explained by rapid population growth after historical founder events (De Meester et al., 2002). Low genetic diversity after colonization by only a few individuals can lead to random genetic drift during parthenogenetic growth. Newly established, fast growing populations can adapt quickly to the local environmental conditions (Allen et al., 2010), and later immigrants face difficulties

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Abbreviations: AFLP, amplified fragment length polymorphism; DOC, dissolved organic carbon.

Location and environmenta	l conditions of lakes of origin.	TOC = total organic carbon	. Pt = platinum.

Tabla 1

Lake	Liasjön	Dammen	Mjöträsket	Torsjön	Kylänalainen
Strains	LI21, LI22	DM18, DM22	MJ12, MJ21, MJ39	TO01, TO13	KY12, KY20, KY23
Location	Southern Sweden	Southern Sweden	Northern Sweden	Southern Sweden	Southern Finland
Longitude	56.762604	56.551346	66.033538	56.762604	60.410038
Latitude	13.990871	14.320550	22.100801	14.906361	23.754930
рН	4.31	6.6	6.91	6.47	5
TOC (mgl^{-1})	30–50	n.a.	6.8	6	5
Water colour					
Absorbance 420 nm, cm ⁻¹	0.256	0.058	0.052	0.041	0.029
$\mathrm{mg}\mathrm{Pt}\mathrm{l}^{-1}$	883	200	179	141	100

to establish, as they have to compete with this locally adapted resident population with higher fitness (Haag et al., 2006). Hence, bottlenecks after founder events are expected to lead to high genetic differentiation among populations (Wade and McCauley, 1988; Whitlock and McCauley, 1990). This hypothesis might also be applicable to microalgae, as most species can rapidly give rise to enormous populations by asexual reproduction.

When gene flow between habitats is restricted, each local population should evolve traits that provide an advantage in its local environmental conditions (Loeuille and Leibold, 2008; Nosil and Crespi, 2004). Adaptation can occur in response to a variety of environmental variables. As these variables structure habitats also on a very fine scale, adaptation allows closely related phytoplankton populations to coexist. Hence, local adaptation by natural selection is an important mechanism for population differentiation (Kawecki and Ebert, 2004). For example, Berge et al. (2011) found evidence for ecotype differentiation in two common dinoflagellate species based on pH adaptation along an oceanic-costal gradient. Rynearson and Armbrust (2004) identified several populations of Ditylum brightwellii (Bacillariophyceae) with distinct genetic and physiological characteristics in closely connected estuaries. On the east coast of the USA a high degree of toxin variability was found in 18 strains of Karlodinium veneficum (Dinophyceae) despite homogenous morphology, genetic data and photopigments, which suggest different functional roles among the coexisting strains (Bachvaroff et al., 2009).

The invasive raphidophyte Gonyostomum semen (Ehrenberg) has aroused much scientific attention in the last decades in Scandinavia (Cronberg et al., 1988; Lepistö et al., 1994; Rakko et al., 2008; Rengefors et al., 2012), as it has spread significantly over the past 50 years from a few lakes in the South to the Arctic Circle. Furthermore, a significant increase in biomass, often connected to extensive blooms in summer, has been reported (Lepistö et al., 1994; Rengefors et al., 2012; Trigal et al., 2013). Cell length ranges from 50 to 100 µm and, despite its high competitiveness, this species is very fragile and grows slowly (0.02–0.08 d⁻¹ observed in nature, Lebret et al., 2012). G. semen is considered a nuisance species, as it alters plankton communities (Angeler and Johnson, 2013) and discharges mucilaginous strands with trichocysts that can cause skin irritations to people swimming in lakes with blooms (Lepistö et al., 1994; Sörensen, 1954). This results in decreased recreational value of the lakes. G. semen was originally described from small lakes and ponds with low pH and high DOC concentration resulting in immediate absorption of short light wavelengths (blue and green) and little light penetration (Drouet and Cohen, 1935; Sörensen, 1954). During the last decades it has also been reported from many non-humic environments with higher pH (Cronberg et al., 1988; Rengefors et al., 2012). Despite this very recent expansion an earlier study by Lebret et al. (2013) reported weak but significant differentiation of this species into genetically distinct populations in Northern Europe.

We hypothesized that *Gonyostomum semen* strains are adapted to the local environmental conditions of their native lake. This may in turn prevent immigration of individuals from other populations and thereby restrict gene flow. To test if strains were locally adapted we performed controlled laboratory experiments, in which we monitored the growth rates of different strains in gradients of pH, DOC concentration and light intensity. These environmental variables were chosen as lakes with regular occurrence of *G. semen* vary significantly in these parameters. However, bloom formation of this species is usually correlated to low pH and high DOC concentrations (Rengefors et al., 2012; Trigal et al., 2013). Adaptation to acidic conditions and low light intensities, which are found at high DOC levels, might give *G. semen* a competitive advantage over many other algal species.

2. Materials and methods

2.1. Sampling and culturing

In these experiments we used clonal Gonvostomum semen cultures, which were established from several lakes in Fenno-Scandinavia in August 2010 and 2011. We chose two strains from the lakes Liasjön, Dammen and Torsjön in Southern Sweden, three strains from lake Mjöträsket in Northern Sweden and three strains from lake Kylänalainen in Southern Finland. Lake Liasjön is characterized by a low pH and high DOC concentrations (Table 1). Lake Kylänalainen has a low pH as well, but low concentrations of DOC, which results in little absorbance and deep penetration of light in this lake (Table 2). The Swedish lakes Dammen, Torsjön and Mjöträsket have intermediate pHs and DOC concentrations. The water temperature at the day of sampling varied between 18 °C and 23 °C. The microalgae were sampled with a plankton net (mesh size 20 μ m) from the shore of each lake and filtered directly through $150 \,\mu m$ mesh to remove large zooplankton, which might feed on G. semen. Single cells were isolated by micropipetting under an inverted microscope (Nikon Eclipse TS100, Melville, New York, USA) and transferred into 96well plates filled with a 300 μ l mixture (1:1) of artificial medium

Table 2	2
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Depth (cm), where experimental light intensity equals light intensity in lakes of origin.

Lake	Absorbance (420 nm, cm ⁻¹)	Light intensity $(\mu mol photons m^{-2}s^{-1})$				
		250	150	25	10	5
Liasjön	0.256	5	5	8	12	17
Dammen	0.058	22	24	37	52	74
Mjöträsket	0.052	24	27	41	58	83
Torsjön	0.041	31	34	52	73	105
Kylänalainen	0.029	43	48	74	103	148

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