

## Estimating the effects of ocean acidification-induced behavioral shifts on primary production of *Heterosigma akashiwo*

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### Abstract

Primary production rates of the toxic raphidophyte *Heterosigma akashiwo* were estimated when laboratory observations of a pH induced downward shift in vertical swimming behaviors were included. Based on empirical measurements of irradiance, cell distributions and specific primary production rates, total water column production decreased to  $1.02 \times 10^{-4}$  mg C m<sup>-2</sup> h<sup>-1</sup> or by 62% due to lower irradiance at depth when pH induced downward swimming was factored into calculations under an ocean acidification scenario. Even inclusion of significantly increased specific primary production rates in a warm and acidified ocean did not negate a decrease in primary production due to downward swimming. If these laboratory predictions apply to the complex conditions in a coastal ocean, the results imply a lower probability of surface slick formation and blooms of *H. akashiwo*.

*Keywords: Heterosigma akashiwo, Ocean acidification, Motility, Population distribution, Primary production*

### Introduction

The average pH of the ocean has decreased due to dissolution of excessive atmospheric carbon dioxide (CO<sub>2</sub>). The resulting decrease in pH has been termed ocean acidification – a decrease by 0.1 units since the pre-industrial era and a further decrease by a further 0.3 to 0.4 units is predicted by 2100 (Zeebe and Wolf-Gladrow 2001; Caldeira and Wickett 2005; Orr *et al.* 2005). Several studies have investigated the impacts of ocean acidification on various aspects of phytoplankton physiology and ecology, including effects on community composition, calcification rates, photosynthesis, growth rates, and primary production (Kleypas *et al.* 2006; Fu *et al.* 2008; Gao *et al.* 2012).

Changes in the marine carbonate system may also affect harmful algal bloom (HAB) species. For example, Fu *et al.* (2012) predicted an increase in toxicity of some HAB species. Increased growth, carbon fixation and primary production rates have been measured under warm and acidified conditions for the toxic raphidophyte, *Heterosigma akashiwo* (Y. Hada Y. Hada ex Y. Hara et M. Chihara) (Clark and Flynn 2000; Fu *et al.* 2008).

From laboratory experiments, we observed significantly enhanced downward motility in *H. akashiwo* in response to lowered pH (Kim *et al.* 2013). Based on these observations, an advection-diffusion model predicted that at lowered pH the

population would undergo a downward shift and fewer cells aggregated at the surface compared to current pH condition (Kim *et al.* 2013). Our study also confirmed prior observation of a pCO<sub>2</sub> fertilization effect on *H. akashiwo* (Fu *et al.* 2008) evident by a 17% increase in growth rates. The effects on primary production rates of a downward shift in the population but higher growth rates in response to lowered pH are unknown.

Here we investigated the relative effects of 1. downward motility, that results in decreased light exposure, and 2. pCO<sub>2</sub> fertilization on total primary production rates of *H. akashiwo*. We found that downward shifts of the population ultimately led to lower estimates of primary production rates for this HAB alga, despite the pCO<sub>2</sub> fertilization effect at lower pH.

### Material and Methods

In a prior study, motility parameters including vertical velocity and diffusivity were quantified from 3-dimensional individual swimming tracks collected in 1L water columns from free swimming *H. akashiwo* cells exposed to pH conditions reflecting pre-industrial (280 ppm), current (380 ppm) and future (750 ppm) atmospheric pCO<sub>2</sub> concentrations (Kim *et al.* 2013). These empirical movement data were used to predict population

distributions of *H. akashiwo* as a function of pH treatment using an advection-diffusion model (Kim *et al.* 2013).

Primary production rates were calculated based on two different *H. akashiwo* population distributions: constant cell concentration with depth termed “uniform”, and the distribution predicted by our model as a function of pH, labelled according to pCO<sub>2</sub> condition (e.g. “750 ppm”). In addition, we examined the combined effects of higher temperature and 750 ppm termed “greenhouse” on primary production rate estimates.

Calculations used the cellular chl-*a* concentration of *H. akashiwo* ( $5.23 \times 10^{-6}$  mg chl-*a* cell<sup>-1</sup>) from Fredrickson *et al.* (2011) and surface irradiance (*E*) ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  or  $\mu\text{E}$ ) of 1250 from measurement in East Sound Washington, USA in July 2007 (Menden-Deuer and Fredrickson 2010). The biomass-normalized primary production rates of *H. akashiwo* was calculated following Jassby & Platt (1976):  $P^B(E) = P_{\text{max}}^B \tanh(\alpha E / P_{\text{max}}^B)$ , where the photosynthetic performance parameters such as the maximum photosynthetic rate ( $P_{\text{max}}^B$ ) (mgC (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup>) and light utilization coefficient ( $\alpha$ ) (mgC (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> ( $\mu\text{E}$ )<sup>-1</sup>) of *H. akashiwo* measured by Fu *et al.* (2008) (Table 1).

	$P_{\text{max}}^B$	$\alpha$
380 ppm	1.29	0.018
750 ppm	1.33	0.032
Greenhouse	2.14	0.024

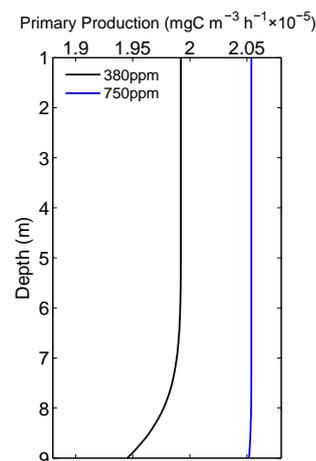
Table 1. Photosynthetic performance parameters measured at different pH and temperature by Fu *et al.* (2008).

Shading of deeper phytoplankton due to shallower aggregations was not considered. Calculations are detailed in Menden-Deuer (2012). All analyses were performed on MATLAB 7.13. Difference in distributions of primary production rates was examined with the Kolmogorov-Smirnov test (K-S test) and a significance level of 0.05.

## Results and Discussion

For uniform with depth *H. akashiwo* distributions and a surface irradiance of 1250  $\mu\text{E}$ , primary production was invariant in most of the water column due to sufficient light availability and slightly higher at higher pCO<sub>2</sub> concentration (Fig. 1). Decay in primary production with depth was only evident at surface irradiance of 150  $\mu\text{E}$  (data not shown). In contrast, when *H. akashiwo*

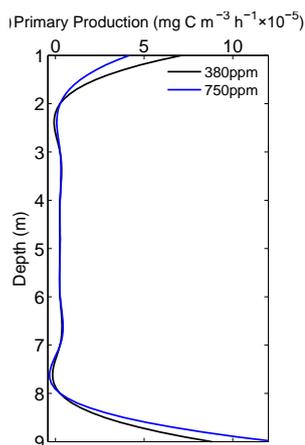
distributions were modelled to be bimodal with a smaller peak at the subsurface and the largest abundance at depth due to pH induced downward swimming, volume specific primary production rates reflected this shift in cell distribution (Fig. 2). Although depth specific primary production rates were significantly different (all  $p < 0.001$ ) between 380 and 750 ppm, the magnitude of the difference was slight (4%).



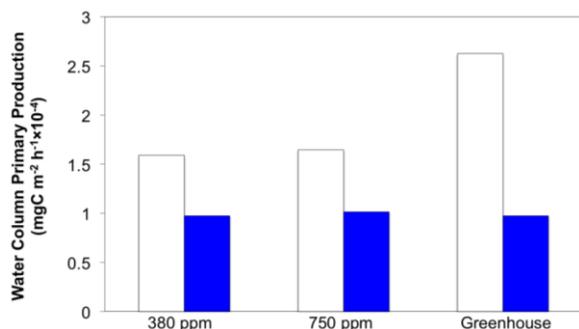
**Fig. 1.** Vertical profile of primary production ( $\text{mg C m}^{-3} \text{ h}^{-1}$ ) of *H. akashiwo* in a 9-m water column with surface irradiance of 1250  $\mu\text{E}$ . Predictions were based on a uniform with depth cell concentration.

When estimates were based on downward shifted population distributions, due to pH effects, vertical profiles indicated that primary production was higher at the surface and at 9-m depth compared to uniform distribution estimates because of denser cell concentrations regardless of pH conditions. For instance, in current pH 40.5 and 45.5% of cells were found at the surface and 9-m, respectively. Under acidified condition, this distribution changed to 22.5 and 67.5% at the surface and 9-m, respectively. Although more cells were found in deeper layers, they were exposed to a lower light intensity ( $\sim 100 \mu\text{E}$ ).

Irrespective of surface irradiance level, the depth-integrated primary production in the water column was highest based on greenhouse condition, whereas differences between 2 pH conditions were relatively small (Fig. 4). As a function of pH and temperature conditions, primary production was saturated at different light levels. Primary production at greenhouse condition was light saturated at higher surface irradiance ( $> 800 \mu\text{E}$ ), whereas primary production was light saturated at surface irradiance near 500  $\mu\text{E}$  irrespective of pH conditions.



**Fig. 2.** Vertical profile of primary production ( $\text{mg C m}^{-3} \text{h}^{-1}$ ) of *H. akashiwo* in a 9-m water column with surface irradiance of  $1250 \mu\text{E}$ . Surface and depth aggregations resulted from behavioural responses of cells to lower pH.

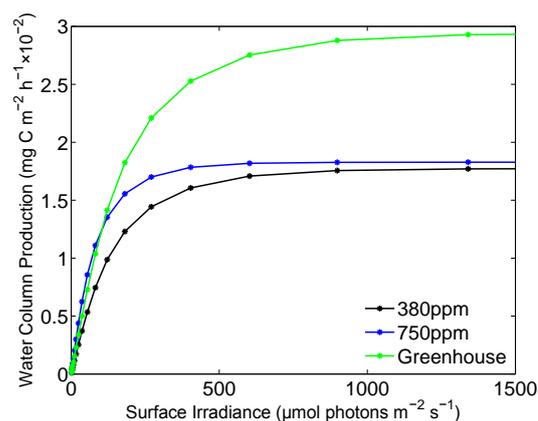


**Fig. 3.** Integrated water column primary production ( $\text{mg C m}^{-2} \text{h}^{-1}$ ) of *H. akashiwo* as a function of pH/temperature and vertical population distribution, estimated at a surface irradiance of  $1250 \mu\text{E}$ . The rates based on a uniform with depth cell concentrations (white bars) were always higher than the rates based on behavioural responses of cells to lower pH (blue bars).

Thus, downward shifts in population abundance would only reduce primary production rates at surface irradiance of  $< 500 \mu\text{E}$ .

## Discussion

This analysis showed that behavioural responses to changed pH conditions, leading to a downward shift in population distribution, resulted in a nearly 62% decrease in depth integrated primary production. This decrease is largely due to decreased exposure to light for *H. akashiwo*, which were found deeper in the water column in acidified condition.



**Fig. 4.** Relationship of integrated water column primary production estimates ( $\text{mg C m}^{-2} \text{h}^{-1}$ ) as a function of surface irradiance levels ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ).

For any of the population distributions, differences in total primary production between current and acidified conditions were not as large as the effects of a shift in population distributions. This may imply that altered behaviour and resulting downward shifted population distributions in decreased pH condition have important ramifications for primary production and bloom formation potential of this HAB species. Primary production via photosynthesis leads to growth and determines growth rates of the bloom-forming alga. A number of studies have reported increased growth rates of *H. akashiwo* under acidified condition (Clark and Flynn 2000; Fu *et al.* 2008; Kim *et al.* 2013), which might be explained based on this alga's absence of a carbon concentrating mechanism (Nimer *et al.* 1997). Fu *et al.* (2008) showed that carbon fixation rates of *H. akashiwo* also increased under acidified condition. This could be interpreted that under future acidified conditions *H. akashiwo* may have a greater growth potential. However, those rates were examined assuming invariant light availability. Given that the population of *H. akashiwo* were shifted towards deeper layers in acidified condition (Kim *et al.* 2013), our finding implies that increased growth rates and primary production of *H. akashiwo* in decreased pH do not necessarily lead to an increase in primary production. The downward shift resulted in considerable lowering of light exposure, which would be exasperated if we assumed lower surface irradiances. It is noteworthy that in a salinity stratified estuary, cells at depth would also be subject to higher predation pressure (Harvey and Menden-Deuer 2012; Strom *et al.* 2012).

Our laboratory analysis of *H. akashiwo* motility was made in the dark over 6 hrs to reduce alterations of ambient pH due to respiration. Thus, we do not know how motility would change in response to prolonged darkness or in alternating light dark regimes. In addition, the assumption used in our study that there is a uniform distribution of *H. akashiwo* in the water column does not take into account natural variability in algal distributions and community structure. Given these limitations, this analysis suggests that anticipated increases in *H. akashiwo* primary production due to increased CO<sub>2</sub> availability are negated by decreases in light availability to cells moving to deeper waters in response to lowered pH.

Application of photosynthesis parameters based on warm and acidified conditions did lead to significant increases in estimated primary production rates. However, a downward shift in population abundance nonetheless lowered estimates by >50%. If applicable to the complex coastal oceans, our results imply a lowered likelihood of the characteristic surface slicks that constitute HAB formation by this raphidophyte alga (Taylor and Haigh 1993). These results make observations of *H. akashiwo* distributions in the coastal ocean and assessment of the relative rates of primary production and grazer induced losses, including in response to manipulated conditions that mimic climate change projections paramount.

### Acknowledgements

This research was supported through funding from the National Science Foundation (Bio OCE 0826205).

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