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Modeling the influence of initial density and copper exposure on the interspecific competition of two algal species

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ABSTRACT

The interspecific competition among algal species is an important process that can change the community structure in aquatic ecosystems. However, there is still a lack of understanding of the impact of various factors on interspecific competition. In this study, both experimental and mathematical modeling approaches were employed to investigate how various combinations of the initial cell densities of *Pseudokirchneriella subcapitata* and *Chlorella vulgaris* and copper exposure levels affect interspecific competition between these species. In the simulation results, *C. vulgaris* appeared to be superior to *P. subcapitata* in the absence of copper exposure. However, in the copper-exposed groups, the competitive positions of both algal species varied with the initial cell density and the copper exposure level. In particular, at the highest copper concentration (10 μg/L), *C. vulgaris* became less competitive than *P. subcapitata* in most initial cell density combinations, resulting in a shift in competitive dominance. This study clearly showed that the dominant species in the interspecific competition could be altered by the two factors studied herein. The developed model provided a more detailed and intuitive understanding of the effects of the two factors on the interspecific competition by simulating the competition at various combinations of initial algal density and copper exposure levels. In this study, the initial algal density and copper exposure levels were selected as the factors influencing the interspecific competition between *P. subcapitata* and *C. vulgaris*, but the proposed model could be used to study the effects of other toxicants on the interspecific competition between other algal species.

1. Introduction

Interspecific competition is one of the fundamental processes determining community structure (Chase et al., 2002), which in turn alters ecosystem function. In particular, an interspecific competition is observed more frequently in aquatic ecosystems than in terrestrial ecosystems (Connell, 1983), and the interactions among prey are known to have a significant impact on high-level predator populations (Garvey et al., 1994). Since algae play a crucial ecological role in freshwater ecosystems as the basis of many food chains and primary producers (Stoiber et al., 2012), it is important to understand interspecific competition among algal species. Intensified interspecific competition between algal species can lead to reduced growth of individuals, resulting in succession and shifts in algal community structure. Furthermore, the impacts of algal competition are likely to cascade through trophic levels (Granéli et al., 2008), which in turn eventually alter the biodiversity and community structure of freshwater ecosystems.

Several studies have demonstrated that various factors, such as allelochemicals (Hulot and Huisman, 2004), nutrition (Chakraborty et al., 2008), initial algal cell density (Tameishi et al., 2009; Qiu et al., 2011), predators (Carusela et al., 2009), and toxicants (Lürling and Roessink, 2006), are involved in algal species competition. Among these factors, allelochemicals, which are the chemical substances released by the algal species for inhibiting the growth of the other algal species, and initial cell densities are the most widely studied. Several algal species can have competitive dominance over others by producing allelochemicals (reviewed by Granéli et al., 2008). Tameishi et al. (2009) and Qiu et al. (2011) reported that the initial densities had a significant impact on the interspecific competition between *Prorocentrum minimum/Skeletonema costatum* and *Chattonella antiqua/Akashiwo sanguinea*, respectively, but Kuwata and Miyazaki (2000) reported no significant effect of the initial densities of *Microcystis novacekii* and *Scenedesmus quadricauda* on interspecific competition. Although

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conflicting results have been reported in the literature, the initial algal cell density can have a significant direct or indirect impact on algal competition as it is linked to the quantity of the allelochemicals produced and preoccupancy/exploitation of limited nutrients (Hulot and Huisman, 2004). Another important factor is the presence of exogenous toxic substances. Algal populations are frequently exposed to various toxicants in the environment, and are one of the most toxicant-sensitive biota among aquatic organisms (Stoiber et al., 2012). Thus, because different algal species have different sensitivities, the dominant species in an aquatic ecosystem could change through the replacement of the sensitive species by the more resistant one (Lürling and Roessink, 2006). Toxicants could be an even more important factor than the other factors involved in algal species competition because they have adverse effects on both species simultaneously. Although the above-mentioned factors might affect the interspecific competition among algae species in a complex manner, no studies have considered the combined effects of these factors.

Since there are limits to experimentally observing the effects of various combinations of factors on the interspecific competition between algal species, a mathematical model can be a useful tool. However, to date, no mathematical model has taken into account the influences of both initial algal densities and toxicants on algal competition. The model proposed by Uchida et al. (1999) has been widely used to study the effects of initial algal density on interspecific competition (Yamasaki et al., 2007; Tameishi et al., 2009; Qiu et al., 2011). However, it is difficult to include the effects of other factors because the interactions between two algal species are simply represented by a single parameter as an interaction rate. On the other hand, the model proposed by Fergola et al. (2007) describes an allelopathic interaction in more detail by adding extra information on how an allelochemical concentration affects the interspecific competition, but no other factors were considered (DellaGreca et al., 2010). In addition, several models have been used to study the effects of specific factors on algal competition (*e.g.*, nutrient limitation: Chakraborty et al., 2008; predators: Carusela et al., 2009), but these models cannot be used to study the influence of initial algal density and toxicants on interspecific competition. Since the structure of a mathematical model depends on the research subjects, a new modeling approach is necessary to improve the understanding of how the combination of initial algal density and toxicants affect algal competition.

Therefore, in this study, a new mathematical model was proposed, and the influence of initial algal density and toxicant on interspecific competition was evaluated. Two freshwater algal species, *Pseudokirchneriella subcapitata* (formerly known as *Rhaphidocelis subcapitata* and *Selenastrum capricornutum*) and *Chlorella vulgaris,* were selected as model species because of their ecological relevance and availability (Silva et al., 2009; Machado et al., 2015). The production of an allelopathic substance (called chlorellin) by *C. vulgaris* makes it ideal for investigating the allelopathic competitive interactions (Fergola et al., 2007). Copper was chosen as a toxic substance because of its frequent detection in aquatic environments and high toxicity to various algal species (Flemming and Trevors, 1989).

The objective of this study was to investigate how various combinations of initial cell densities of two algal species, *P. subcapitata* and *C. vulgaris*, and copper exposure affect interspecific competition in a closed system through both experimental and mathematical modeling approaches. The conceptual diagram for interspecific competition between the two algal species and the flowchart of the study processes are shown in Fig. 1. To obtain the data sets for model calibration, various combinations of initial cell densities of both algal species were monitored periodically over time under copper exposure conditions (0, 5, and 10 μg/L). A mathematical model, including the effects of initial density, copper exposure levels, and allelopathy, was developed in order to explore their combined effects on the interspecific competition between the two algal species. Using the experimental data sets, the model was calibrated to predict the density dynamics of the two algal species over time, and the interspecific competition between the two species was evaluated in terms of competitive dominance, competitive response, and time required to reach the maximum algal density.

2. Experiments

2.1. Test algae and culture conditions

Two freshwater microalgal species *P. subcapitata* (strains CCAP 278/4) and *C. vulgaris* (strains AG40003) were obtained from the Culture Collection of Algae and Protozoa (CCAP, Scottish Marine Institute, UK) and the Korean Collection for Type Cultures (KCTC, Korea Research Institute of Bioscience and Biotechnology, Korea), respectively. The growth medium was prepared in accordance with the United Stated Environment Protection Agency (EPA) method 1003.0 (EPA, 2002). Both algal species were maintained in separate 200-mL Erlenmeyer flasks containing 100 mL of synthetic algal medium (EPA, 2002). The flasks were incubated at 20 ± 1 °C with a 16-h light/8-h dark photoperiod under illumination at 70 μmol photons/m^2/s with cool white fluorescent light (TLD 30 W, Philips). The maximum densities of *P. subcapitata* and *C. vulgaris* were approximately 4.0×10^6 and 4.0×10^7 cells/mL, respectively, under these culture conditions. The flasks were hand-agitated twice daily to minimize flocculation and clumping of algal cells. All glassware used in the algal culture maintenance and experiments were completely immersed in 10% nitric acid for at least 1 d and was thoroughly rinsed with distilled water before use.

2.2. Experimental designs

The copper stock solution was prepared by dissolving the reagent-grade copper (II) sulfate pentahydrate ($CuSO_4{\cdot}5H_2O$, ≥99% purity, Sigma-Aldrich) in the synthetic algal medium. The stock solution was diluted with the synthetic medium to make the final copper concentrations of 5 and 10 μg/L. These copper concentrations were selected based on our previous study (unpublished data) in which the growths of *P. subcapitata* and *C. vulgaris* were severely inhibited when exposed to 15 μg/L or higher concentrations of copper. In addition, Franklin et al. (2002) reported that the 72 h EC_{50} values of copper for the growth inhibition of *P. subcapitata* and *Chlorella* sp. were 17 and 16 μg/L, respectively. The pH values of the test solutions were adjusted with 0.1 M HCl or 0.1 M NaOH to remain in the range of 7.5 ± 0.1.

To investigate how various initial cell density combinations of *P. subcapitata* and *C. vulgaris* affect the interspecific competition in either the presence (treatments) or absence of copper exposure (control), algal growth experiments were conducted in 100-mL glass beakers filled with 70 mL medium with several combinations of initial cell densities. To adjust the initial cell density of each species, both algal species were harvested at steady growth phase by centrifuging at 600 × *g* for 5 min and then resuspended in the growth medium. The initial cell densities of *P. subcapitata* and *C. vulgaris* were adjusted to range from 3.0×10^4 to 3.5×10^5 cells/mL and 2.0×10^5 to 4.0×10^6 cells/mL, respectively (Table 1). The combinations of initial cell densities were determined to include various *P. subcapitata*/*C. vulgaris* ratios in the estimation of model parameters. As reported previously (Hu and Zhang, 1993; Franklin et al., 2002), the initial cell density was set to a relatively high value in adverse conditions (*i.e.*, copper exposure). In each combination, five replicates were performed.

During the experiments, all beakers were sealed with Parafilm (polyethylene) to prevent the evaporation of the test medium, and were kept at the same environmental conditions as those used for culture maintenance. The beakers were shaken by hand twice a day. The algal cell densities were checked periodically (1–16-d interval) over the 78 days until the algal cell density in each beaker was close to zero. The number of algal cells in each combination was counted using a hemocytometer (Marienfeld, Germany) under an optical microscope (E200;

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