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Trophic linkage of a temperate intertidal macrobenthic food web under opportunistic macroalgal blooms: A stable isotope approach

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ABSTRACT

The effects of blooms of opportunistic green macroalgae, *Ulva prolifera*, on the trophic structure of the macrobenthic food web in a temperate intertidal zone on the western coast of Korea were evaluated using carbon and nitrogen stable isotopes. Biomasses of *Ulva* and microphytobenthos (MPB) increased significantly at the macroalgae-bloom and the non-bloom sites, respectively, from March to September 2011. The δ^{13}C values of most the consumers were arrayed between those of MPB and *Ulva* at both sites, and differed according to feeding strategies at the macroalgae-bloom site. Seasonally increasing magnitudes in δ^{13}C and δ^{15}N values of consumers were much steeper at the macroalgae-bloom site than at the non-bloom site. Our findings provide evidence that blooming green macroalgae play a significant role as a basal resource supporting the intertidal macrobenthic food web and their significance varies with feeding strategies of consumers as well as the resource availability.

1. Introduction

Nutrient enrichment in coastal waters has been accelerated due to increased anthropogenic activities and has led to mass blooms of green macroalgae, i.e., an extraordinary proliferation of fast-growing macroalgae (Fletcher, 1996; Raffaelli et al., 1998; Corzo et al., 2009). These macroalgae are generally ephemeral species, primarily comprising filamentous and unattached green algae, and blooms of these species are becoming increasingly common on intertidal flats and shallow subtidal areas in coastal environments worldwide (Valiela et al., 1997; Teichberg et al., 2010). Because of their ecological and economic consequences, often as nuisance blooms, much attention has long been paid to the occurrence, regulating factors, and impacts of macroalgal blooms (Raffaelli et al., 1998; Teichberg et al., 2010).

As opportunistic species, ephemeral macroalgae belonging to the genera *Ulva* and *Enteromorpha* have an advantage in taking up nutrients under high nutrient loading and are thus better adapted to coastal environments with their rapid growth (Pederse and Borum, 1997; Pihl et al., 1999; Teichberg et al., 2010). These opportunistic macroalgal blooms have different direct and indirect effects on ecosystem structure and function, as they can modify physical and biological factors by forming mats with their abundant and dense canopies (Raffaelli et al., 1998; Jones and Pinn, 2006). In addition, they tend to accumulate in large amounts on the sediment after blooms, and proceed through bacterial decomposition that may affect the microbiology and chemistry of the sediment (Valiela et al., 1997; Raffaelli et al., 1998; Corzo et al., 2009). These physical and biogeochemical changes have significant influences on the abundance and diversity of the microphytobenthic (Sundbäck et al., 1996) and benthic meio/macrofaunal communities (Norkko and Bonsdorff, 1996; Jones and Pinn, 2006; Bohórquez et al., 2013). Consequently, such changes in the major component levels of an ecosystem can lead to the modification of whole food web structure through bottom-up control (Raffaelli et al., 1998; Patrício and Marques, 2006; Ouisse et al., 2011). However, because most environmental disturbances modify food web structure on different scales based on the degree of their spatiotemporal variability (Vizzini and Mazzola, 2006; Ouisse et al., 2011; Kanaya et al., 2013), knowledge about the trophic functions of blooming ephemeral macroalgae in benthic food webs is still lacking.

Organic matter in coastal ecosystems is derived from a variety of autochthonous and allochthonous sources (McLusky, 1989). Identifying trophic functions of specific primary producers and assessing the trophic bases supporting food webs in coastal ecosystems are of primary concern in understanding ecosystem functioning. In this respect, the stable isotope techniques allow us to elucidate the trophic transfer of organic matter and structure of coastal food webs, providing time- and space-integrated insight into the consumer diet (Layman et al., 2012). This method is based on the assumption that the stable carbon

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and nitrogen isotope signatures of consumer tissues reflect those of assimilated dietary sources, with predictable trophic enrichments of <1‰ for carbon and 2–4‰ for nitrogen through metabolism (Post, 2002; Boecklen et al., 2011; Layman et al., 2012). In general, major primary producers in temperate coastal regions have distinct $\delta^{13}C$ and $\delta^{15}N$ values from each other. Previously reported $\delta^{13}C$ values for microphytobenthos (MPB, −20‰ to −10‰) and marine phytoplankton (−24‰ to −18‰) in coastal waters are more negative than that (on average −10.5‰ for *Ulva pertusa*) of green macroalgae (Kang et al., 2003; Wang and Yeh, 2003; Yokoyama et al., 2005; Park et al., 2015). Their $\delta^{15}N$ values may also vary depending on the source of inorganic nutrients that they assimilate (McClelland and Valiela, 1998; Cole et al., 2004; Mutchler et al., 2004). Anthropogenic sources of inorganic nitrogen lead to higher $\delta^{15}N$ values of primary producers than internal source of uncontaminated coastal waters does. Accordingly, $\delta^{13}C$ and $\delta^{15}N$ signatures of consumers exposed to green macroalgal blooms can highlight how coastal food web is modified by environmental disturbance of this kind (Schaal et al., 2010; Olsen et al., 2011; Kanaya et al., 2013).

The western coast of the Korean peninsula bordering the Yellow Sea hosts some of the largest tidal flats in the world and receives great attention in a variety of fields of tidal flat research (Koh and Khim, 2014). Hampyeong Bay, located on the southwestern coast of Korea, constitutes a sheltered bay system with an extensive intertidal zone that occupies >50% of the entire bay area (Waska and Kim, 2011). Although there is little river input and a small volume of surface runoff, green macroalgal blooms composed of *Ulva prolifera* seasonally occur rather frequently in the southern intertidal zone within the bay (Hwang and Koh, 2012). However, little is known about the effect of the seasonal proliferation of *U. prolifera* on the trophic base and food web structure of the intertidal macrobenthic communities. In the present study, we analyzed the stable carbon and nitrogen isotope ratios of dominant macrobenthic consumers and major primary producers during two contrasting seasons in *Ulva* biomass at the macroalgae-bloom sites of the intertidal flat in Hampyeong Bay, making comparison with those at the non-bloom sites. Our null hypothesis was that $\delta^{13}C$ and $\delta^{15}N$ of consumers would be identical between the macroalgae-bloom and the non-bloom sites. We also tested whether the trophic base of the intertidal food web depends on the seasonal variation in the macroalgal biomass. Our major goal was to assess the effect of ephemeral macroalgal blooms on the trophic functioning of the benthic ecosystem in a broad intertidal zone.

2. Materials and methods

2.1. Study area

Hampyeong Bay is located on the western coast of Korean peninsula; the maximum width is 8.5 km, the length is 17 km, and the total area is 85 km^2 (Fig. 1). The bay is a typical sheltered embayment system with a main channel and a narrow mouth, and it is relatively shallow, with a mean depth of 4 m at high tide (Ryu, 2003). The tide is semidiurnal, and the mean tidal range is 3.5 m, with maximum tidal amplitudes of 4.6 m on spring tides (Waska and Kim, 2011). Because of the narrow bay mouth and large tidal amplitudes, strong tidal currents of >1 m s^{-1} can appear in the main channel, with a maximum depth of 23 m (Ryu, 2003). Extensive tidal flat, which is composed mainly of mud and muddy sand transported into the bay from the Yellow Sea, has developed along both sides of the bay. In the intertidal zone, sediments are characterized by mud and sand bodies (e.g., sand bars and cheniers) as well as mixed types (Ryu, 2003). In particular, groundwater seeps out of coarse-grained sediments and the ephemeral macroalga (*U. prolifera*) forms visible patches on the intertidal flat during low tide (Waska and Kim, 2011). The maximum area covered by the macroalgae has been estimated as 3.2 km^2 within the bay by satellite images. Submarine groundwater discharge is reported to be a major nutrient source for benthic and pelagic primary production in the bay, as there are no river inputs, and precipitation (annual total ~1125 mm) is commonly concentrated during the summer monsoon season (Waska and Kim, 2010, 2011).

2.2. Field sampling and laboratory processing

Sampling was carried out in two contrasting intertidal habitats: ephemeral macroalgae-bloom and non-bloom sites. Macrobenthic consumers and their potential food sources were collected from two replicate sites in each habitat in March and September 2011. To collect suspended particulate organic matter (SPOM) for stable isotope analysis, 20-L water samples were collected at the main channel on flood tides using a van Dorn water sampler and then triplicate samples were immediately prefiltered through a 200-μm mesh sieve to remove any zooplankton and large particles. The water samples were filtered through precombusted (450 °C for 4 h) Whatman GF/F glass fiber filters. For chlorophyll *a* (chl *a*) analysis of the water column, 1-L water samples were filtered through GF/F filters (Whatman, 47 mm diameter)

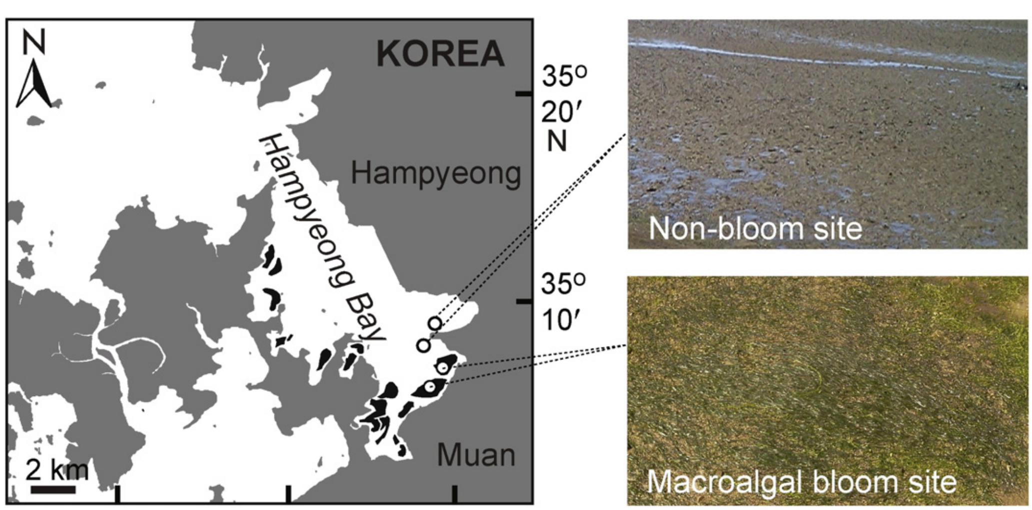

Fig. 1. Map of the sampling sites in Hampyeong Bay. Black-colored areas represent macroalgae-bloom sites covered by *Ulva prolifera*.