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Response of suspension-feeding clams to natural removal of bioturbating shrimp on a large estuarine intertidal sandflat in western Kyushu, Japan

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ABSTRACT

On a 3.4-km^2 intertidal sandflat in Ariake Sound, Japan, four phytoplankton-feeders were dominant in the benthic community in terms of abundance and biomass in spring–summer, 2004: ghost shrimp, *Nihonotrypaea japonica*, mud shrimp, *Upogebia major*, and clams, *Ruditapes philippinarum* and *Mactra veneriformis*, each occupying a specific one-fourth area of the sandflat. *N. japonica* is a deposit feeder, while the others are suspension feeders. *N. japonica* and *U. major* dwell in 0.7- and 2-m deep burrows, respectively. Subsequent monitoring conducted every spring during 2005 to 2008 revealed that (1) probably due to typhoon- and stingray-induced substratum disturbances for mud and ghost shrimp populations, respectively, these had greatly shrunk from their original mid- to low-tide habitat in 2005 and high- to mid-tide one in 2006, respectively, (2) vacated space was colonized by juveniles of both clams and a formerly subdominant, suspension-feeding clam, *Meretrix lusoria*, (3) only *Ma. veneriformis* and *Me. lusoria* were found as adults there, with *R. philippinarum* adults remaining limited to the low-tide zone, and (4) loss in sum total population biomasses due to that in the shrimp' was compensated by the gain in the clam species'. These findings suggest that the five species compete for (1) space, with superiorities exerted by shrimps to clams through the former's intense bioturbating activities and by *Ma. veneriformis* and/or *Me. lusoria* to *R. philippinarum* in the high- to mid-tide zone and vice versa in the low-tide zone, and (2) food to the limit of the carrying capacity provided by the sound. Furthermore, estimates were made of the benthic community biomass in the past based on a long-term record (or estimate) of chlorophyll-*a* concentrations (proxy measure for food) for the sound water column and of the *R. philippinarum* population biomass based on its fishery-landing record. The latter estimate would account for 60% of the former one in the late 1970s, when the first eutrophication is believed to have been in progress. The subsequent decrease in benthic community biomass was suggested in response to that in phytoplankton abundance, reaching the one-fourth level in 2004–2008. In the long run, three alternative states would have occurred in the benthic community, from (1) *R. philippinarum* population boom in the 1970s, through (2) remarkable increases in the populations of the shrimps and *Ma. veneriformis* in place of *R. philippinarum* in the early to mid-1980s, followed by a plateau until 2004, to (3) the one described here for the 2004–2008 period.

1. Introduction

Macrobenthic community structure in estuarine and coastal soft-sediment habitats is determined by both physical and biological factors. The latter involves predation, competition, and facilitation, which are often mediated by bioturbation or alteration of sediment physico-chemical properties (Commito and Ambrose, 1985; Constable, 1999; Foreman et al., 1995; Meysman et al., 2006; Reise, 2002; Woodin, 1983). Of large macrobenthos on estuarine tidal flats, ghost shrimp (Decapoda: Axiidea: Callianassidae) and mud shrimp (Decapoda: Gebiidea: Upogebiidae) are known for exerting marked influences on benthic communities and ecosystem functions through construction of deep burrows and intense bioturbating activities (Atkinson and Taylor, 2005; Felder, 2001). Ghost shrimps extrude significant amounts of sediment out of their burrow openings associated with deposit feeding as well as burrow construction processes, making the substratum surface erodible (Berkenbusch and Rowden, 1999; Murphy, 1985; Pillay et al., 2007a,b; Tamaki, 1988) and the sediment column less compact (Miller and Myrick, 1992; Wardiatno et al., 2003). By contrast, once their burrow formation is accomplished, mud shrimps expel little sediment outside and make the surrounding substratum hard by consolidating the inner burrow wall with mucus and mud (Dworschak, 1987; Kinoshita et al., 2003; Posey et al., 1991; Wynberg and Branch, 1994). Both ghost and mud shrimps powerfully ventilate and irrigate their burrows (Griffen et al., 2004; Stamhuis and Videler, 1998), which are conducive to oxygenating and oxidizing the surrounding sediment

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(Bertics and Ziebis, 2009; Volkenborn et al., 2012) and to enhancing microbial decomposition and mineralization of organic matter (Jordan et al., 2009; Kinoshita et al., 2003; Papaspyrou et al., 2005). Combinations of the above processes positively or negatively affect other members of the benthic community to set a limit to determine the abundance and distribution of those affected species including suspension-feeding bivalves (Flach and Tamaki, 2001; Pillay and Branch, 2011).

Another limit for the abundance and distribution of macrobenthos in soft-sediment habitats is set by the total amount of food supply and its partitioning among members of the benthic community. The latter process can be realized through competition for space which partly involves sediment-mediated interactions. The suspension-feeding for microalgae is one major feeding mode among macrobenthos including bivalves such as clams, cockles, mussels, and oysters. In well-mixed shallow estuaries, the total biomass of the suspension-feeder assemblage can be limited by the system primary productivity, and its members can compete for food (Dame et al., 2001; Herman et al., 1999). In mildly eutrophied coastal and estuarine waters of the North Sea and its surrounding areas, the increase in phytoplankton abundance in the late 1970s was followed by an increase in total macrobenthic biomass with a time lag of one or more years (Austen et al., 1991; Beukema et al., 2002; Josefson et al., 1993). These findings are an outcome of long-term monitoring studies in respective sites. Thus, a first ideal step to determine the reality of the limit mentioned above would be to find whether the carrying capacity of a soft-sediment habitat for macrobenthos, as reflected on their sum total biomass value, varies depending on the amount of food supply. The second step would be to examine how the allocation of the total macrobenthic assemblage biomass into component species' populations varies according to the temporal change in their densities and distributions within that habitat. For tidal flats, only a few snapshot studies have been conducted regarding detailed two-dimensional biomass distributions among the phytoplankton-feeding assemblage over a large area (Hanekom et al., 1988; Tamaki et al., 2008), nor been their temporal dynamics.

Ariake Sound, situated in mid-western Kyushu, Japan, is a well-mixed meso-tidal estuary with a mean water depth of 20 m, a number of large tidal flats along its shoreline, and a mean freshwater residence time of 2.1 months (Yanagi and Abe, 2003). On an intertidal sandflat sandwiched between the mouths of two rivers in the middle of the sound (hereafter called Shirakawa sandflat after the larger river name; 32°47′N; 130°36′ E; Fig. 1A, B), four large-sized species were the dominant members of the infaunal community during 1999 to 2004 (Nakano et al., 2012; Tamaki et al., 2008; Wardiatno et al., 2003; Yokoyama et al., 2005b), comprising the callianassid shrimp, *Nihonotrypaea japonica* (Ortmann, 1891), the upogebiid shrimp, *Upogebia major* (De Haan, 1841), the surf clam, *Mactra veneriformis* Deshayes (Reeve, 1854), and the Manila clam, *Ruditapes philippinarum* (Adams & Reeve, 1850). The last species is one of the most important invertebrate fishery resources in Japan. The two shrimp species are representative bioturbators, exhibiting only a little overlap in their distributions with each other most probably due to contrasting effects on the substratum (*N. japonica* as a destabilizer to soften versus *U. major* as a stabilizer to harden it: Tamaki et al., 2008). In recent years, the population of the venerid clam, *Meretrix lusoria* (Röding, 1798), another important fishery resource in Japan, has grown to join the dominants of the benthic community (Nakamura et al., 2010). Carbon and nitrogen stable-isotope analysis has demonstrated that all five species depend solely on phytoplankton (Yokoyama et al., 2005a,b). Only *N. japonica* is a deposit feeder, subducting deposited phytoplankton and/or fresh phyto-detritus, and the other four species are suspension feeders (Tamaki et al., 2008). Tamaki et al. (2008) have suggested that in 2004, *N. japonica*, *U. major*, *Ma. veneriformis*, and *R. philippinarum* would be competing for space and food under the carrying capacity of the sandflat, as evident in a roughly non-overlapping distribution pattern of both individual densities (each one-fourth occupation in area) and biomass densities over the sandflat. Furthermore, based on unpublished information available from the two local fisheries cooperative associations which govern and regulate clam harvest on the Shirakawa sandflat [Oshima and Matsuo Fisheries Cooperative Associations (abbreviated as OFCA and MFCA), personal communication] and on published information for other intertidal sandflats in Ariake Sound, Tamaki et al. (2008) depicted a scenario regarding the long-term succession of the Shirakawa-sandflat benthic community since the 1960s such that (1) the annual commercial landings of the Manila clam had increased until the late 1970s probably owing to the progress of eutrophication in the sound, attaining a peak value of 3830 metric tons in 1979, (2) thereafter, the landings have continuously decreased to reach, in 2004, the one-eighth of the peak value, (3) in the 1970s, Manila clams were distributed over the sandflat, dominating over the other three potential competitors, and (4) in the 1980s and afterwards, both density and distribution range of the other three species have increased. It is possible that *Me. lusoria* could become involved in the present competitive system.

Most recently on the Shirakawa sandflat, the population sizes of *U. major* and *N. japonica* have rapidly decreased to become almost nil eventually, probably due to intense physical and biological substratum disturbances, respectively (A. Tamaki et al., personal observation): (1) on 7 September 2004, a typhoon (annual registration no. 18 by Japan Meteorological Agency) came close to the sandflat, inducing unusually high waves for Ariake Sound (F. Yamada, unpublished data; Nakano et al., 2012) to expel a large number of *U. major* individuals out of their burrows (Fig. 2A), which fell preys to gulls (Fig. 2B) or harvests to local people on the subsequent exposure hours; and (2) the decline of the *N. japonica* population might have been caused by continual predation impact from the stingray (elasmobranchs), *Dasyatis akajei* (Müller & Henle, 1841), of which dense and widespread feeding pits markedly increased in recent years (Fig. 2C, D; at times stingrays were left alive in shallow pools on the exposed sandflat). Callianassid shrimps co-occur with ray pits in intertidal-flat habitats (D'Andrea et al., 2004; Martinell et al., 2001; Myrick and Flessa, 1996) and are reported to be a major prey item for stingrays (Ebert and Cowley, 2003; Harada and Tamaki, 2004; Howard et al., 1977; Tillett et al., 2008). A possible competitive release from these shrimp populations would have afforded the three dominant clam species a chance to enlarge their population sizes on the Shirakawa sandflat. The impact of the mud shrimp and/or ghost shrimp on tidal-flat benthic communities has been assessed on relatively small spatial scales by a combined approach of (1) observing the species and density compositions between plots with lower and higher densities of these shrimps in space and/or time and (2) conducting shrimp exclusion or transplant experiments in the field (Berkenbusch et al., 2000; Como et al., 2004; Dittmann, 1996; Murphy, 1985; Peterson, 1977; Pillay et al., 2007a,b, 2008; Posey, 1986; Posey et al., 1991; Skilleter et al., 2005; Tamaki, 1994; Tamaki and Suzukawa, 1991; Wynberg and Branch, 1994). Larger spatial-scale exclusions of mud or ghost shrimp populations (e.g. over an entire tidal flat) have rarely been undertaken. Such an attempt was carried out for the ghost shrimp, *Neotrypaea californiensis*, and the mud shrimp, *Upogebia pugettensis*, by pesticide application on estuarine tidal flats in the Pacific coast of Northwest America, which was aimed at increasing the yield of oysters raised on the ground (Dumbauld et al., 2006). In the same geographic region, a wide-scale collapse of that mud shrimp population was caused by the infection with an exotic bopyrid isopod parasite (Chapman et al., 2012). So far community-level effects from these shrimp losses have not been reported. The present natural "experiment" on the Shirakawa sandflat, with extensive removal of mud and ghost shrimp populations, would provide us with a unique opportunity to observe the subsequent change in density and distribution of the three potentially competitively inferior clam species belonging to the same phytoplankton-feeding assemblage.

The objective of the present study was to describe the change in the distribution of both individual and biomass densities of juvenile and adult clams of *Ma. veneriformis*, *R. philippinarum*, and *Me. lusoria* over the Shirakawa sandflat in the Ariake-Sound estuary for a four-year