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Stable isotope ratios reveal food source of benthic fish and crustaceans along a gradient of trophic status in the East China Sea



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ABSTRACT

The East China Sea (ECS) receives large quantities of particulate organic matter (POM) and inorganic nutrients transported from the Changjiang (Yangtze River), which have produced high productivity in the northwestern ECS. This study evaluated potential contributions of terrigenous POM (allochthonous food source) and nutrient-induced marine production (autochthonous source) to the ECS benthic ecosystem by analyzing stable isotopic compositions of phytoplankton, zooplankton, benthic crustaceans and fish. Benthic consumers exhibited $\delta^{13}C$ values similar to those of their autochthonous food sources (i.e., phytoplankton and zooplankton), revealing their major reliance on marine production. In contrast, the δ^{13} C values of benthic fish (-19.6% to -13.5%) and crustaceans (-18.9% to -15.0%) were much higher than that of terrigenous POM (-25.7%), which generally accounted for less than 20% of the most fish diet. Phytoplankton and zooplankton generally exhibited higher δ^{13} C values at eutrophic and highly productive inshore sites than at oligotrophic offshore sites. This enrichment of inshore δ^{13} C values was mainly attributed to lower photosynthetic fractionation during algal blooms, an effect that was further enhanced during flood period of the Changjiang. The δ^{13} C values of demersal fish assemblages were also significantly higher at inshore sites and decreased seaward. However, fish δ^{15} N values and their estimated trophic levels showed relatively small spatial variation. The disproportionate variations in δ^{13} C and δ^{15} N values suggested that the enriched C isotopic signatures derived from an elevated δ^{13} C baseline of the inshore food web instead of trophic enrichment of the isotopic ratios. The significantly positive correlations between concentrations of chlorophyll a and nutrients versus fish δ^{13} C provided further evidence for the use of pelagic algal bloom materials by inshore consumers. The isotopic and oceanographic survey data suggested that inorganic nutrients discharged from the Changjiang River nourish benthic consumers in the ECS and play an important role in linking marine benthic ecosystems to local pelagic primary production as well as to the adjacent terrestrial watershed.

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1. Introduction

Coastal ecosystems adjacent to large rivers are tightly connected to terrestrial environments via large inputs of freshwater and materials. River inputs of nutrients greatly accelerate the growth of marine primary producers and nitrogen loadings are positively related to fisheries yields (Nixon et al., 1986). Understanding how marine communities utilize river-discharged materials is important for tracing energy flow and resources distribution from terrestrial to marine ecosystems (Antonio et al., 2010). During past decades,

anthropogenic activities have caused catastrophic changes in large rivers and the adjacent marginal seas, principally by overenrichment of nutrients (Nixon, 1995; Diaz, 2001). The global nitrogen and phosphorus fluxes from rivers to coastal oceans have grown more than two- to threefold over the past half century, resulting in more than 760 coastal areas undergoing eutrophication (Howarth et al., 1995; Galloway et al., 2004; Diaz et al., 2011). Nutrient-promoted phytoplankton blooms may positively nourish the local biota by providing organic matter (Graf, 1992; Nascimento et al., 2008), yet these blooms also may harm marine ecosystems by causing hypoxic conditions (Breitburg, 2002; Grall and Chauvaud, 2002). Though eutrophication generally originates in pelagic ecosystems, the effects of increased organic deposition, accelerated oxygen consumption, and modified habitat structure can transcend

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ecosystem boundaries (Grall and Chauvaud, 2002; Vadeboncoeur et al., 2003). Therefore, both the marine pelagic and benthic communities in the sea areas abutting rivers are susceptible to the effects of terrigenous nutrients.

The East China Sea (ECS) has experienced severe eutrophication since the 1960s due to the dramatic increase of nutrient fluxes from the third longest river in the world – the Changjiang (Yangtze River). Concentrations of dissolved inorganic nitrogen (DIN) and phosphate in the Changjiang water have risen more than five-fold between the 1960s and the end of 1990 (Wang, 2006). In the late 1990s more than 1.4×10^6 t vr⁻¹ of inorganic nitrogen was conveved from the Changijang into the ECS (Gao and Wang, 2008). The nutrient overload increased the occurrence of spring algal blooms in the Changjiang estuary and ECS from less than 10 times per year to more than 80 times per year between the 1930s and 2000s (Zhou et al., 2008). Though the frequent algal blooms were thought to be deleterious by causing bottom-water hypoxia (Chen et al., 2007) and by damaging benthic communities (Chang et al., 2012), these bloom materials also could act as nutritious food for marine secondary producers and contribute to higher trophic consumers in the ECS ecosystem, particularly in the Changjiang freshwater impacted area (isohaline of salinity 31) where the highest algal biomass was observed (Gong et al., 2011).

Riverborne organic materials also have the potential to nourish benthic consumers. Terrestrial particulate organic matter (POM) could be incorporated by marine benthic food webs and contribute to fishery catches via ingestion by local macrofauna, such as molluscs, crustaceans and polychaetes (Gearing et al., 1991; Riera and Richard, 1996; Bouillon et al., 2000; Darnaude et al., 2004). The Changjiang annually transports about 4.4×10^6 t of particulate organic carbon to the adjacent ECS (Dagg et al., 2004; Gao and Wang, 2008). The transported terrigenous particles could travel more than 250 km from shore (Wu et al., 2007a), thus potentially providing an alternative food source for the benthic consumers across the continental shelf. It remains unclear whether the ECS benthic consumers would concurrently utilize the autochthonous (marine primary production) and allochthonous organic matter (riverborne POM), and which the main food source is.

Stable carbon and nitrogen isotope analyses have been successfully applied to clarify trophic structure with multiple food sources (Minagawa and Wada, 1984; Peterson et al., 1985). The δ^{13} C signal of terrestrial POM is generally isotopically lighter by 5–6% than marine production and the δ^{13} C undergoes little change (approx. 1%, Peterson et al., 1985) during transmission through trophic levels. Thus, carbon isotopic ratio is increasingly applied to explore linkages between riverine material and marine ecosystems (Voss and Struck, 1997). The C isotope variability of consumers along the terrestrial-estuarine-marine gradient indicates a natural enrichment trend of $\delta^{13}C$ values from estuarine to coastal areas in riverinfluenced ecosystems such as the observations in Thames Estuary and Louisiana coastal waters (Leakey et al., 2008; Fry, 2011). This enrichment ranged from about 3% for POM (Fry and Wainright, 1911) to more than 7% for benthic fish (Leakey et al., 2008) depending on the geographical scales of sampling, levels of fluvial influence, or trophic status of the environment. This increasing trend indicates both the mixing of terrestrial and marine organics and the significant differences in the baseline isotopic signatures along this spatial gradient because the carbon isotopic composition of primary producers would be modified in different nutrient regimes (Gearing et al., 1991; Savoye et al., 2003). In highly eutrophic and productive systems, the photosynthetic fractionation between DIC and organic C is often reduced, thus elevating the δ^{13} C values of primary producers (Cifuentes et al., 1988). Stable nitrogen isotopes could assess organisms' trophic positions because consumers tend to have higher $\delta^{15}N$ than their foods by an average of 3-4% (Minagawa and Wada, 1984; Post, 2002). The dual isotope approach is thought to be reliable for investigating trophic structure (Post, 2002). Therefore, by analyzing the carbon and nitrogen isotopic compositions of food sources and consumers, the spatial and temporal variations in food utilization by benthic consumers across the ECS shelf may be clarified.

Spatial differences in benthic communities' diets are greatly determined by the shift in relative availabilities of food sources (Antonio et al., 2010, 2012). In the ECS, amounts of both algal bloom materials and riverborne POM are most concentrated in the Changiliang mouth and inshore waters and rapidly decrease seaward (Wu et al., 2003, 2007a; Gong et al., 2011). Therefore, we hypothesized that the benthic consumers may exhibit a spatial dietary shift from mixed food sources of terrestrial POM and marine production in the inner shelf to mono-source of in situ marine production in the outer shelf. By analyzing the isotopic compositions of demersal fish and crustaceans across the ECS continental shelf, we may ascertain how food utilization by benthic consumers varies along a trophic gradient. Moreover, determining the spatial variability in energy uptake by benthic consumers across an extensive shelf with land-based influence may allow further prediction about the effects of environmental changes on the benthic ecosystems.

2. Materials and methods

2.1. Study sites and sample collection

The demersal fish and benthic crustaceans were repeatedly collected from the ECS in July of 2008, 2009 and 2010. The details of sampling methods have been described in Chang et al. (2012). The surveyed sites encompassed large spatial scale and trophic gradients from the eutrophic inshore area to the mesotrophic and oligotrophic outer shelf (Fig. 1). The inshore sites (i.e. < 150 km from the land, sites O1, A1, B1, C1) were generally shallower than 60 m and influenced by Changjiang freshwater discharge (Table 1). The trawled fish and benthos were frozen on board immediately and identified to species in the laboratory. Stable isotopic composition of several fish and crustacea species were determined. For the benthic crustaceans (decapoda and Stomatopoda), only the individuals collected from sites A1–A3 in July 2008 were analyzed.

In order to distinguish marine production from terrestrial POM, isotopic compositions of phytoplankton communities from both inshore and offshore sites in July 2009 and 2010 were analyzed (Fig. 1). Surface water samples from each station were first filtered

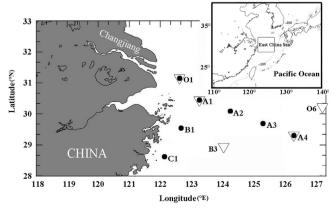


Fig. 1. Sampling sites for benthic consumers (ullet), phytoplankton and zooplankton ($^{\circ}$) in the East China Sea.

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