

Molluscan response to early Pleistocene rapid warming in the Sea of Japan

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ABSTRACT

Major changes occurred in the benthic molluscan fauna of the Sea of Japan continental shelf during the transition from Pleistocene glacial to interglacial stages, owing to rapid warming associated with the inflow of the warm Tsushima Current. Molluscan associations representing this transition occur in the lower Pleistocene Omma Formation in central Japan and suggest that there were two patterns of faunal change. The first was when warm-water species migrated into the Sea of Japan and lived along with cold-water species, accompanied by a northward shift in species ranges. The second pattern involved the migration of warm-water mollusks shortly after the local extinction of cold-water species. In the latter, it is possible that benthic molluscan communities with very low diversity and density existed temporarily and locally at inner shelf depths (<100 m) during the warming phase. Such a community has no modern analogue, but may have resulted from a marine climate with a higher seasonality than occurs today. These findings show that episodes of rapid warming have severe impacts on offshore benthic communities and molluscan species that include patterns not represented by modern faunal distributions.

Keywords: early Pleistocene, molluscan communities, Sea of Japan, obliquity, rapid warming.

INTRODUCTION

Understanding biotic responses to rapid climate change during the Quaternary affords key insights for modeling and planning for possible future human-induced climatic change (Overpeck et al., 1992; Valentine and Jablonski, 1993; Faunmap Working Group, 1996; Roy et al., 1995, 1996; Cronin and Raymo, 1997; Cannariato et al., 1999). These studies have shown that species tend to respond in a Gleasonian model (Gleason, 1926) to climatic fluctuations by migration. In this model it is assumed that species respond in ecological time to environmental change in accordance with their individual tolerance limits. Thus, migrations have resulted in significant changes in terrestrial and benthic marine faunas, often producing associations having no present-day analogues. These geologically temporary faunal associations were likely caused by climatic conditions that differ from the modern state (Webb et al., 1987; Overpeck et al., 1992). Increased knowledge of biotic responses to rapid climate change during the Quaternary has been based largely on data from North America and Europe. In contrast, few studies have addressed faunas in other temperate areas and the relatively monotonous offshore environment. In order to understand the response of offshore fauna of the Northwest Pacific to environmental change, we examined faunal changes among early Pleistocene marine mollusks associated with rapid warmings within ten 41 k.y. obliquity driven climate cycles in the Sea of Japan.

EARLY PLEISTOCENE FOSSIL RECORD IN THE SEA OF JAPAN

The Tsushima Current, a branch of the warm Kuroshio Current, enters the Sea of Japan through Tsushima Strait and makes its way northward along the western coast of Honshu Island (Fig. 1). The current supplies a large quantity of heat into the Sea of Japan. Therefore, the current likely had a profound influence on the Quaternary paleoclimate and ecosystem within and around the Sea of Japan (e.g., Oba et al., 1991).

According to Ishiwatari et al. (1999), the alkenone-based sea-surface temperature measured in sediment cores from the Oki Ridge shows a sharp increase from 14 °C at 11.6 ka to 19 °C at 11.1 ka, as the warm Tsushima Current began to flow into the Sea of Japan. The warming rate was less than that predicted for future warming, but is very high for the Quaternary of Japan. The rapid warming may have affected the shallow water along the west coast of Honshu and thus may have strongly influenced organisms there. However, no study has been done on faunal change

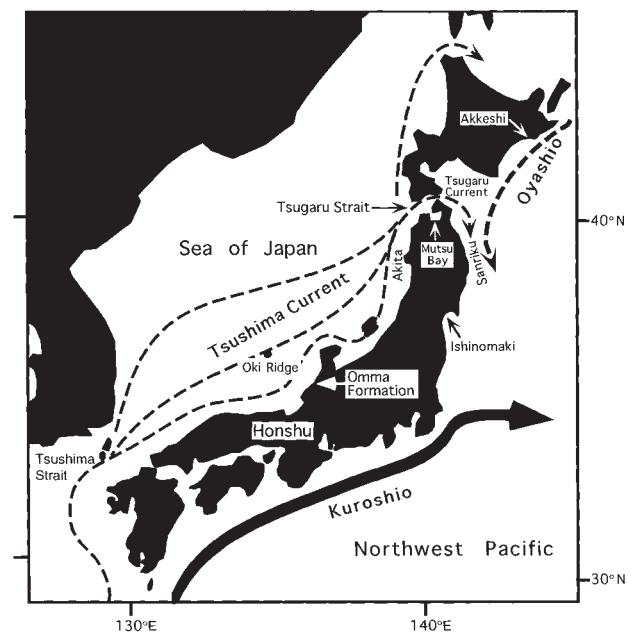


Figure 1. Map of Sea of Japan and surrounding region, showing location of Omma Formation.

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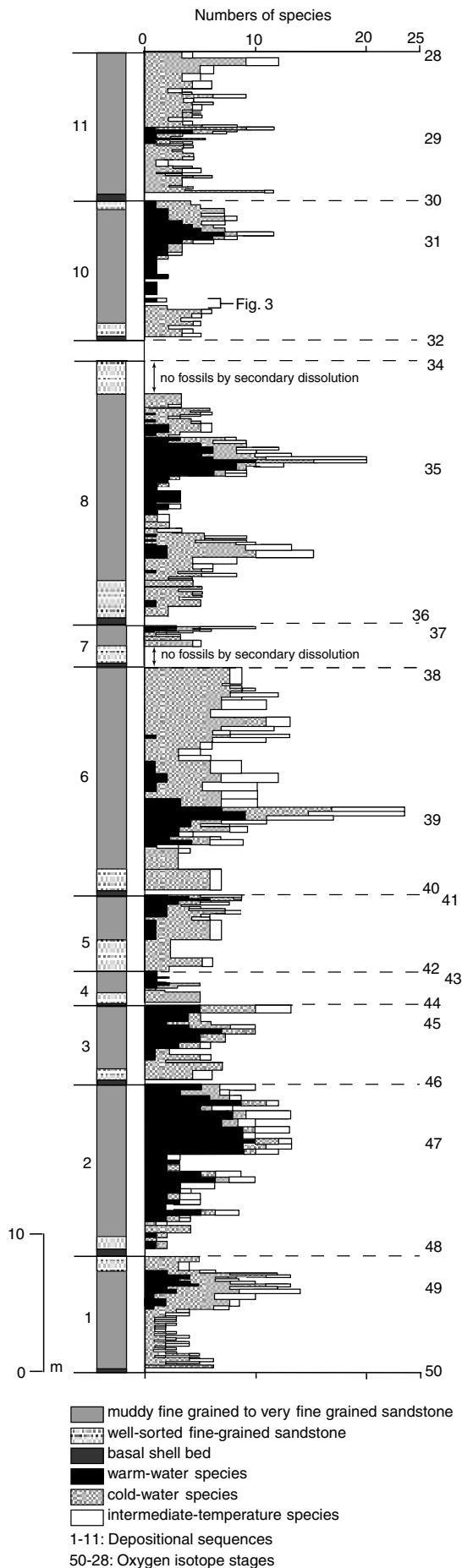


Figure 2. Stratigraphic distribution of mollusks in 11 6th-order (41 k.y.) depositional sequences of lower Pleistocene Omma Formation that accumulated during oxygen isotope stages 50 to 28.

during the past 12 k.y. on the continental shelf of the Sea of Japan, because neither sediment nor fossil records for this period had been collected. The Tsushima Current has flowed into the Sea of Japan during interglacial stages since oxygen isotope stage 49 (Kitamura et al., 1994). Many early Pleistocene molluscan species still live in the Sea of Japan. Thus, the pattern of faunal response to rapid warming during the early Pleistocene transition from glacial to interglacial stages may be similar to that of ca. 11 ka. We here present the stratigraphic distribution and abundance of environmentally sensitive benthic mollusks collected from the lower Pleistocene Omma Formation, a deposit that accumulated on the continental shelf in the Sea of Japan.

The Omma Formation crops out around Kanazawa City along the western coast of central Japan (Fig. 1). The formation at its type section (exposed along the Saikawa River at Okuwa) has been divided into lower, middle, and upper parts. The middle part is composed of 11 sixth-order (41 k.y.) depositional sequences that accumulated during oxygen isotope stages 50 to 28 (Kitamura et al., 1994). These depositional sequences, numbered 1 to 11 from oldest to youngest, consist mainly of inner shelf sediments deposited in water depths <100 m (Kitamura et al., 1999). Depositional sequence 9 is not exposed at the type locality. Within a representative sequence, in situ molluscan faunal changes indicate that marine conditions changed from cold-water, upper-sublittoral to warm-water, lower-sublittoral, followed again by cold-water, upper-sublittoral conditions (Kitamura et al., 1994). We therefore examined the responses of molluscan species to rapid warming for 10 stage transitions (Fig. 2).

METHODS

The stratigraphic distribution and abundance of 99 molluscan species collected from the middle part of the Omma Formation at the type section was described by Kitamura (1991, 1995) and Kitamura et al. (1994, 1999) as well as this study. There are two modes of occurrence of fossil mollusks in the Omma Formation. The first is within a shell bed at the base of a depositional sequence, and the other consists of in situ mollusks in sandstone. Mollusks in the basal shell bed were excluded from this study because they were reworked from older deposits. All individuals of the in situ mollusks in sandstone were identified and counted from a rectangular block of sandstone 1.0 m long parallel to strike and 0.5 m wide. The thickness of the block ranged from 5 to 50 cm due to the uneven surface of the exposures. Figure 2 shows the pattern of faunal change with numbers of species from the sandstone block.

Stratigraphic variations in the distribution of the mollusks indicate that there were two patterns of faunal change in response to warming. The first is represented by the co-occurrence of warm- and cold-water species within a single stratigraphic horizon. The second mode is when the stratigraphic distribution of both warm and cold faunas is separated by an interval barren of mollusks. The barren zone has a maximum thickness of 30 cm (depositional sequence 10), and its existence is significant for understanding biotic responses to rapid warming. In order to learn more about the paleoenvironment, we examined the stratigraphic distribution of warm-water planktonic foraminifera within the Omma sediments. Planktonic foraminifera were studied from 25 1-cm-thick sediment samples from a 0.7-m-thick stratigraphic interval that includes the so-called barren horizon (Fig. 3). About 200 specimens of planktonic foraminifera were identified and counted per sample from the >125 μm size fraction. The definition of warm- and cold-water species for both mollusks and planktonic foraminifera follows Kitamura et al. (1994) and Takemoto and Oda (1997), respectively. Warm and cold assignments for 17 extinct molluscan species are based on the modern distribution of related living species. All extinct species, except for *Pecten* (*Pecten*)

byoritsuensis, are regarded as cold-water species. According to Amano and Ohno (1988), *P. byoritsuensis* is regarded as a warm-water species.

RESULTS

The appearance of warm-water mollusks occurs in the lower part of the muddy fine-grained to very fine grained sandstone within the Omma depositional sequence (Figs. 2 and 3). An estimate of the time averaging of fossil records is needed when attempting to infer biotic responses to rapid climate change (Faunmap Working Group, 1996; Roy et al., 1996). According to Kitamura (1992), the mixing of skeletal elements was restricted to a surface layer about 20 cm thick during deposition of the muddy fine-grained to very fine grained sandstone. In depositional sequences 1, 3, 5, 6, 7, and 11 (correlated with oxygen isotope stage transitions 50 to 49, 46 to 45, 42 to 41, 40 to 39, 38 to 37, and 30 to 29), the faunal change is represented by the appearance together of warm- and cold-water species (Fig. 2) in horizons 0.5 to 2 m thick. This co-occurrence of warm- and cold-water mollusks is not an artifact of postdepositional mixing. Thus, during inflow of the Tsushima Current into the Sea of Japan, warm-water species appeared and became established, while many cold-water species disappeared, leaving few survivor species.

The number of cold-water species and individuals decreases upsection, and cold-water taxa are absent from depositional sequences 2, 4, 8, and 10 (Figs. 2 and 3). Warm-water species appear 10–30 cm above the disappearance horizon of cold-water species in depositional sequences 8 and 10 (stage transitions 36 to 35 and 32 to 31) (*Acila insignis* in sequence 8; *Yoldia notabilis* in sequence 10) (Fig. 3). These data imply that warm- and cold-water species did not always coexist. Both cold- and warm-water species co-occur in thin horizons within depositional sequences 2 and 4 (stage transitions 48 to 47 and 44 to 43). The horizon in depositional sequence 2 is only 6 cm thick but contains cold-water *Turritella saishuensis saishuensis*, warm-water taxa *Paphia schnelliana*, and *Zeuxis caelatus* and the intermediate-temperature bivalve *Macoma nipponica* (Kitamura et al., 1999). In similar fashion, depositional sequence 4 contains a 20-cm-thick horizon containing the cold-water bivalves *Clinocardium fastosum* and *Y. notabilis* and the warm-water gastropod *Onustus exutus*. However, whereas individuals of *M. nipponica* are preserved in life position, the other bivalves within these thin horizons are disarticulated. Considering the prevalence of disarticulated bivalves in these thin horizons, it is likely that warm-water species did not coexist with cold-water species during the warming phases in depositional sequences 2, 4, 8, and 10. The stratigraphic distribution of dominant planktonic foraminiferal species in depositional sequence 10 is shown in Figure 3.

DISCUSSION

Communities situated on the geographic boundaries between warm- and cold-water faunas commonly include mixtures of both elements (e.g., Jablonski and Valentine, 1990). Co-occurring warm- and cold-water mollusks are reported from Mutsu Bay and off Akita, at the modern northern limit of warm-water mollusks in the Sea of Japan (Ishiyama, 1970; Takayasu and Yunohara, 1977). If this boundary moved northward with warming associated with the Tsushima Current, the molluscan faunal change would be expressed as a pattern of cold-water species declining and warm-water species increasing. Such a transition has been documented in the rocky intertidal communities of Monterey Bay, California, where species adapted to cooler conditions have declined while warm-adapted species have increased with warming over the past 60 yr (Barry et al., 1995). This pattern of faunal change is similar to that in depositional sequences 1, 3, 5, 6, 7, and 11, in which the offshore molluscan fauna contracted their ranges northward in response to inflow of the warm Tsushima Current into the southern Sea of Japan.

There are no co-occurring cold- and warm-water mollusks in depositional sequences 8 or 10. It is noteworthy that intermediate-temperature species are not present in the intervals between the horizon containing cold-

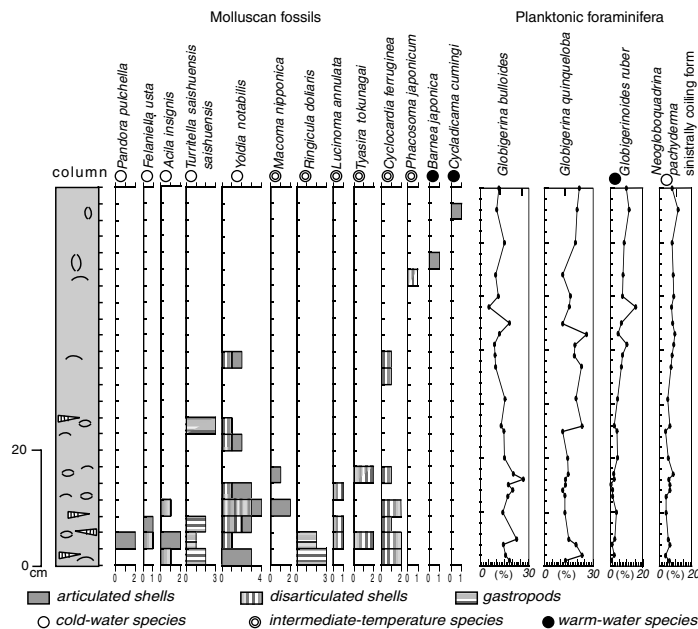


Figure 3. Stratigraphic distribution of mollusks and selected planktonic foraminifera in study section of depositional sequence 10 that accumulated during transition from oxygen isotope stages 32 to 31.

water species and the subsequent appearance of warm-water species in depositional sequences 8 and 10 (Fig. 3). The absence of molluscan fossils within the barren zone may be due to sample size, but similar barren zones are not present in depositional sequences 1, 3, 5, 6, 7, and 11, from which molluscan data were derived using the same sampling technique. Thus, it seems possible that an environmental condition unfavorable for mollusks temporarily prevailed during the warming phase.

As noted here, the mixing of fossil records was restricted to a surface layer about 20 cm thick during deposition of the muddy fine-grained to very fine grained sandstone. The stratigraphic position of the first warm-water planktonic foraminifera is 60 cm below the disappearance of cold-water mollusks in depositional sequence 10 (Fig. 3). Moreover, the occurrence of the dominant warm-water planktonic foraminifer, *Globigerinoides ruber*, suggests good preservation, because its test dissolves relatively easily (Hemleben et al., 1989). These data suggest that the appearance of warm-water planktonic foraminifera preceded the disappearance of cold-water mollusks. Thus, the local extinction of cold-water mollusks was caused by warming due to the Tsushima Current. If the current transported the larvae of warm-water mollusks into the study area, then environmental factors did not allow them to survive. There is no significant change in the planktonic foraminiferal fauna in the interval between the first appearance of warm-water planktonic foraminifera and the later appearance of warm-water mollusks, suggesting that no significant changes took place in factors such as the sedimentation rate, productivity, salinity, or dissolved oxygen. Taken together, these factors suggest that environmental conditions did not allow offshore cold- and warm-water mollusks or intermediate-temperature mollusks to coexist in the study area.

The glacial-interglacial cycles of the early Pleistocene have an obliquity cycle with a period of 41 k.y. The greater is Earth's tilt, the more intense are seasons in both hemispheres; summers get hotter and winters colder. It is significant that the volume of flow of the Tsushima Current is highly seasonal. The maximum volume transported is $5.6 \times 10^6 \text{ m}^3/\text{s}$ in September, or about 5–6 times as much as the minimum volume, which is transported in winter (Isobe et al., 1994). The combination of high obliquity and seasonal volume changes implies high seasonality in bottom-water temperatures. This relationship is supported by the co-occurrence of warm-water planktonic foraminifera *G. ruber* and the cold-water, sinistrally coiling form

of *Neogloboquadrina pachyderma* (Fig. 3). In addition, species living offshore tend to have narrow physiological tolerances (e.g., Jackson, 1974). Thus, we infer that high seasonality resulted in an environment that was unsuitable for both offshore cold- and warm-water mollusks.

The last surviving cold-water mollusc was *Y. notabilis*, and the first warm-water immigrant was either *Barnea japonica* or *Cycladicama cumingi* in depositional sequence 10 (Fig. 3). The stratigraphic position of in situ *B. japonica* is about 10 cm below in situ *C. cumingi*, although this difference may be attributed to differences in their burrowing depths, because *B. japonica* may burrow as deep as 20 cm (Kondo, 1987). The relationship between reproductive cycle and thermal tolerance is unknown for these species, and *B. japonica* is not known to exist in the modern Sea of Japan. Because of this, our inference of unsuitable seasonality based on the geographic distribution of *Y. notabilis* and *C. cumingi* remains tentative. The bivalve *Y. notabilis* is reported from Akkeshi to Ishinomaki along the northwestern Pacific (eastern) shelf of the Japanese Islands (Nakaoka, 1989) (Fig. 1), where it is absent from water masses with a maximum mean monthly temperature $>20^{\circ}\text{C}$. However, the distribution of *C. cumingi* extends through Tsugaru Strait to the northern Sanriku coast, and is influenced by the Tsugaru Current, a branch of the warm Tsushima Current (Ishiyama, 1973) (Fig. 1). On the basis of water temperature alone, the Sanriku coast is substantially north of the northern limit of *C. cumingi*. Mean bottom-water temperatures for March and September in this area are 6°C and 20°C , respectively, and these are the temperature limits for *C. cumingi*. Therefore, the absence of *Y. notabilis* and *C. cumingi* implies winter temperatures lower than 6°C and summer temperatures higher than 20°C . Such high seasonality does not occur on the modern-day continental shelf around the Japanese Islands. In summary, a marine climate having no modern analogues in the Sea of Japan briefly prevailed on the continental shelf during warming associated with inflow of the warm Tsushima Current into the Sea of Japan and resulted in benthic communities with very low density and diversity of mollusks. These fossil patterns indicate that rapid climate transitions have a severe impact on offshore communities and a Gleasonian model is valid to predict the effects of rapid warming on marine communities in this sector of the northwest Pacific.

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