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The sequence of local recolonization of warm-water marine molluscan species during a deglacial warming climate phase: a case study from the early Pleistocene of the Sea of Japan

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Abstract

Changes in the fossil assemblage of offshore molluscs within each sixth-order (41-kyr) depositional sequence of the early Pleistocene Omma Formation document repeated recolonizations of warm-water species into the Sea of Japan. Each recolonization started as soon as the warm Tsushima Current began to flow in the Sea of Japan during a deglaciation and subsequent interglacial period. Here we examined in detail the stratigraphic distribution of six selected significant warm-water species and calculated confidence intervals for their first (local) appearances in a total of 10 deglaciations using continuously sampled data. They were subdivided into two groups, based on the chronological order of their first appearance during warming phases. Comparison of geological with biogeographic data reveals that these migration patterns are not always consistent with the modern geographic distributions of the species. These results show that fossil records may anticipate how the assemblage of local species would change in response to climate warming.

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1. Introduction

Many paleoecological studies in various regions have demonstrated that communities have responded in a Gleasonian manner (Gleason, 1926) to Quaternary climate change (e.g., Overpeck et al., 1992; Roy et al., 1996; Faunmap Working Group, 1996; Jackson and Overpeck,

2000). Based on Gleasonian theory, the manner of the response of each species to environmental change does not accord with an 'ecological succession' (Clements, 1916) but depends on its own specific tolerance. Therefore, modeling the responses of communities to environmental changes throughout the Quaternary period requires an understanding of how each species changes its geographic distribution. During the past few decades, a number of studies have described the changes of molluscan faunas in response to the frequent climatic changes during the Quaternary (e.g., Thomsen and Vorren, 1986; Peacock, 1989;

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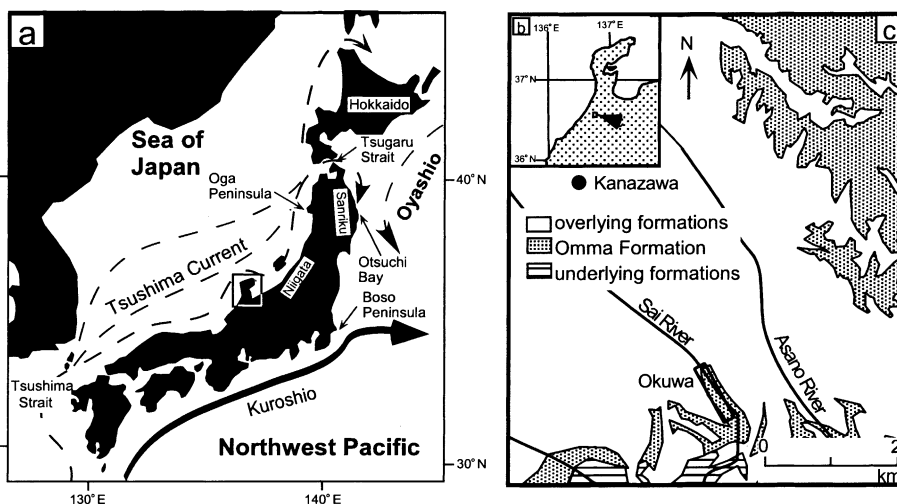


Fig. 1. The Sea of Japan and surrounding region (a), showing the location of the Omma Formation (b and c).

Kanazawa, 1990; Kitamura et al., 1994; Kamataki and Kondo, 1997). However, most of these studies have focused on the replacement of the entire fauna, and little attention has been paid to the timing of migration of each species with climatic change, especially with rapid warming. The present study attempts to clarify the precise pattern of migration for significant warm-water molluscan species during a warming climate phase. The chronological order of the first appearance of such species during seven selected deglaciations in the early Pleistocene of the Sea of Japan provides the data for the study. We estimate confidence intervals for the first (local) stratigraphic occurrences of various warm-water species based on the data of Kitamura (1991) and Kitamura et al. (1999, 2000b), and then determined the timing of recolonization of each species during the seven deglaciations.

2. Geological setting

The planktonic marine $\delta^{18}\text{O}$ record of sediment cores from the Oki Ridge demonstrates an increase of sea-surface temperature from 8–12°C at 10 ka to 17–18°C at 8 ka, showing the beginning of the inflow of the warm Tsushima Current

(Oba et al., 1980). The current has come into the Sea of Japan recurrently during each interglacial stage since oxygen isotope stage 59 (Kitamura et al., 2001). The rapid warming (ca. 3.5°C per 1000 years) caused by the Tsushima Current may have strongly influenced the marine organisms along the west coast of Japanese Islands throughout the past 1.7 Myr.

The early Pleistocene Omma Formation accumulated on the continental shelf of the Sea of Japan (Fig. 1), and contains abundant fossils of benthic molluscs, ostracods and planktonic foraminifers, which are sensitive to environmental changes (e.g., Kaseno and Matsuura, 1965; Ogasawara, 1977; Cronin and Ikeya, 1987; Kitamura and Kondo, 1990; Beu and Kitamura, 1998; Amano and Vermeij, 1998; Kitamura et al., 1999, 2001; Amano and Watanabe, 2001; Ozawa and Kamiya, 2001). The middle part of this formation at the Okuwa type section (Figs. 1 and 2) is composed of 11 sixth-order (41-kyr) depositional sequences (sequence 9 is not exposed) that were deposited in inner- to outer-shelf water depths during oxygen isotope stages 50–28 (Fig. 2) (Kitamura et al., 1994, 2000a; Kondo et al., 1998). These sequences include the following elements, in ascending stratigraphic order: (1) a basal sequence boundary that is superposed on the ra-

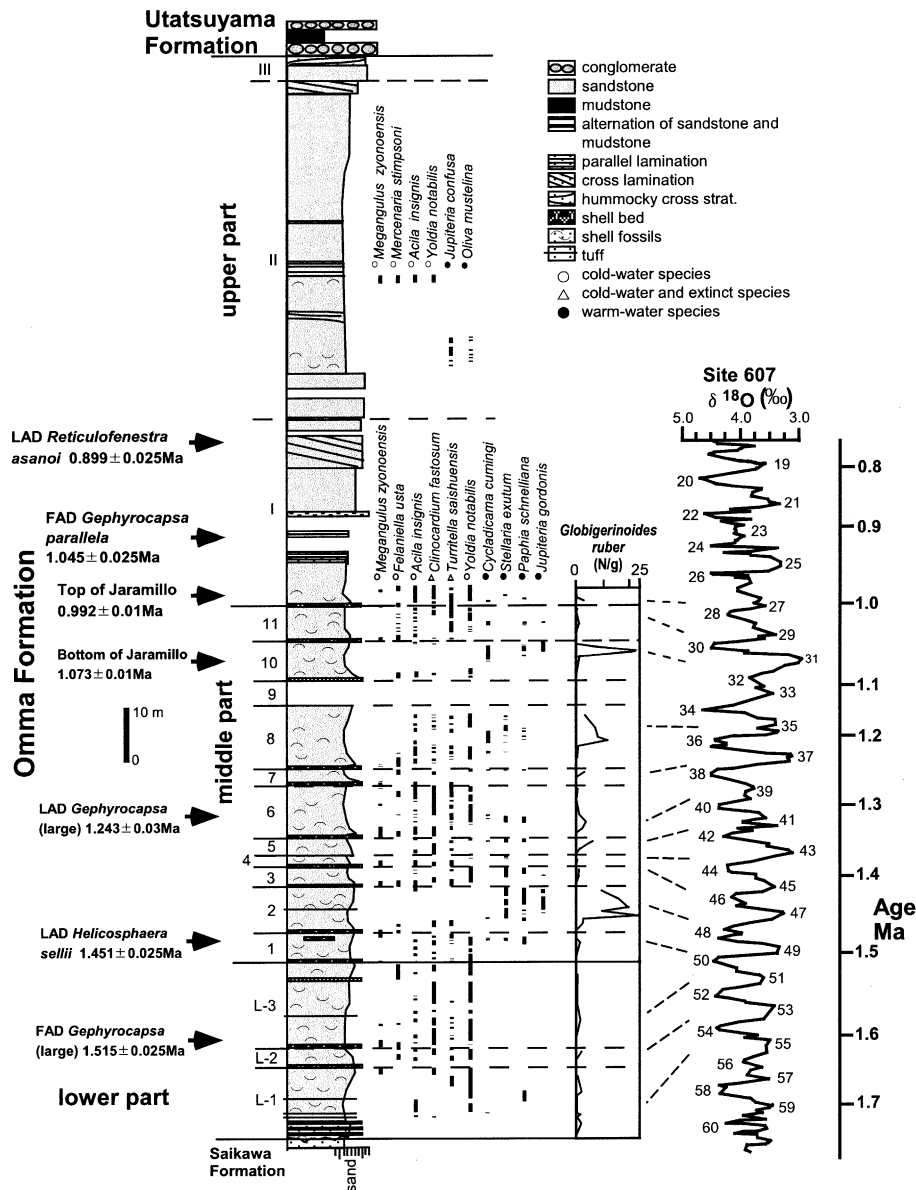


Fig. 2. Comparison between the stratigraphic distribution of molluscan species in the Omma Formation at its type section and the oxygen isotope record at DSDP Site 607 (Ruddiman et al., 1989). Biostratigraphic datum horizons are after Takayama et al. (1988); magnetostratigraphic data are from Kitamura et al. (1994); time scale for the oxygen isotope record at DSDP Site 607, and ages of biostratigraphic datum horizons and magnetic polarity changes are based on the chronology of Berger et al. (1994).

vinement surface; (2) a transgressive systems tract (TST) (2–5 m thick) consisting of a basal shell bed (0.3 m thick) (a condensed onlap shell bed) and overlying fine- to very-fine-grained sandstone; (3) a maximum flooding horizon that has the highest

concentration of sand-size carbonate grains; (4) a highstand systems tract (HST) (2–3 m thick) consisting of fine-grained sandstone and sandy siltstone; and (5) a regressive systems tract (RST) (<1.0 m thick) comprised of a coarsening-up-

ward fine-grained sandstone (Kitamura et al., 2000a). Depositional sequences 1, 6 and 11 include complete sets of TST, HST and RST sediments, while other sequences lack RST and even HST sediments because of shoreface erosion at the superjacent sequence boundary (Kitamura, 1998; Kitamura et al., 2001).

The transition of the offshore molluscan fauna in the TST of each depositional sequence always begins with prominence of the cold-water *Felaniella* Association. Subsequently, the *Felaniella* Association is replaced by the cold-water *Clinocardium-Turritella* Association because of the change in substrate from well-sorted sand to muddy sand associated with deglacial sea-level rise. Finally, either the warm-water *Stellaria-Paphia* I Association or *Cycladicama* Association dominates the fauna. This faunal change was caused by inflow of the warm Tsushima Current and the associated rapid warming (Kitamura et al., 1994, 2000b).

In any depositional sequence, the sediment of the horizon just below the first appearance of warm-water species is a muddy, fine- to very-fine-grained sandstone with mud content ranging from 15 to 25%. This type of sediment layer characteristically yields a cold-water *Clinocardium-Turritella* Association consisting of *Clinocardium fastosum*, *Turritella saishuensis saishuensis*, *Acila insignis* and *Yoldia notabilis*, which inhabited the upper sublittoral zone from the low-water mark to 50–60 m deep (Kitamura et al., 1994, 2001). In other words, a total of 10 immigration events of warm-water molluscs happened under almost the same conditions of sedimentation and water depth. The mollusc assemblages do not contain post-mortem transport of species from other habitats, because many fossil specimens of bivalves are found with their valves articulated. The within-habitat mixing of skeletal elements had been restricted to a surface layer about 10 cm thick throughout deposition of the muddy, fine- to very-fine-grained sandstone at the transition from glacial to interglacial stages (Kitamura, 1992). Using an average sedimentary rate from the three best-preserved depositional sequences (17.5 cm/1000 years), persistence of warm-water species at the studied area is an estimated 5000–

10000 years and time-averaged as about 600 years.

3. Methods

The definition of cold- and warm-water mollusc assemblage of the Omma Formation is based on the modern geographic distribution of living representatives of the species along the continental shelves of Japan. The warm Kuroshio Current veers away from the Japanese Islands at the Boso Peninsula at 35°N latitude (Fig. 1a), which is recognized as a biogeographic discontinuity for marine animals. For this reason, the term ‘warm-water species’, in Japan, has been used to represent the species which live south of 35°N at present, while ‘cold-water’ usually qualifies the species living north of 35°N.

The 50%, 80% and 95% confidence intervals were calculated for the true first appearance of warm-water species within each depositional sequence, according to Marshall (1997). Since the fossil record is generally incomplete, using the observed range of stratigraphic occurrence of a species may lead us to underestimate the true range of the species. The method of assessing the confidence intervals on stratigraphic ranges, pioneered by Strauss and Sadler (1989) and established by Marshall (1990, 1997), allows an estimation of the stratigraphic range of the species in terms of statistics. When the distribution of a fossil horizon is non-random, calculation of the confidence interval on the stratigraphic range of the species requires not only a measure of the number of individuals, but also the fossil recovery potential function. In this case, the method for calculating the confidence interval is applicable only to continuously sampled sections. Consequently, we use the total number of fossils recovered from continuously sampled sections (Kitamura, 1991; Kitamura et al., 1999, 2000b) as a density-distribution function representing the fossil recovery potentiality.

For all in situ specimens examined, each individual was taxonomically identified and the number of individuals within a sample was counted. Each sample consisted of a rectangular sandstone

Horizons	molluscan association	<i>Paphia schnelliana</i>	<i>Stellaria exutum</i>	<i>Zeuxis castus</i>	<i>Cycladicama cumingi</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
5.25-5.55	(1)	0	0	0	0	15	RST
4.8-5.25		0	0	0	0	3	
4.7-4.8	Transitional Association	4	0	0	0	13	HST
4.6-4.7		3	0	1	1	21	
4.5-4.6		0	0	1	0	17	
4.4-4.5		2	1	0	1	12	
4.3-4.4		11	0	1	0	20	
4.15-4.3		3	1	3	0	22	
4.05-4.15		4	2	1	0 ↓ ₅₀	20	
3.9-4.05		4	0	0	0	20	
3.7-3.9		2	0 ↓ ₅₀	1	0	24	
3.4-3.7		1	0	0	0	17	
3.2-3.4	0	0	1	0	13		
3.05-3.2	0 ↓ ₅₀	0 ↓ ₈₀	2	0	15		
2.9-3.05	0	0	1	0	18		
2.75-2.9	0 ↓ ₈₀	0	0	0	6		
2.6-2.75	0	0	0	0	4		
2.5-2.6	0	0	0	0	3		
2.4-2.5	0	0	0 ↓ ₅₀	0	7		
2.3-2.4	0	0	0	0	4		
2.2-2.3	0	0	0	0	1		
2.1-2.2	0	0	0	0	6		
2.0-2.1	0	0	0	0	4		
1.9-2.0	0 ↓ ₉₅	0	0	0	2		
1.8-1.9	0	0	0	0	4		
1.7-1.8	0	0	0	0	5		
1.6-1.7	0	0	0 ↓ ₈₀	0	4		
1.5-1.6	0	0	0	0	6		
1.4-1.5	0	0	0	0	5		
1.3-1.4	0	0	0	0	4		
1.2-1.3	0	0	0	0	11		
1.1-1.2	0	0	0	0	6		
1.0-1.1	0	0	0	0	6		
0.9-1.0	0	0	0 ↓ ₉₅	0	5		
0.8-0.9	0	0	0	0	4		
0.7-0.8	0	0	0	0	7		
0.6-0.7	0	0	0	0	9		
0.5-0.6	0	0	0	0 ↓ ₈₀	2		
0.4-0.5	0	0	0	0	7		
0.3-0.4	0	0	0	0	17		
0.2-0.3	0	0	0	0	13		
0.1-0.2	0	0 ↓ ₉₅	0	0	21		
0.0-0.1	0	0	0	0	11	TST	

Fig. 3. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 1 of the Omma Formation. The total numbers of molluscan fossils include those of cold-water, extinct cold-water and intermediate species. Transitional association consists of a mixture of both cold- and warm-water elements. Horizons represent the level (m) above the top of the basal shell bed. Gray shaded areas indicate observed stratigraphic ranges. Lines represent: double line, bottom of the 50% confidence interval; broken line, bottom of the 80% confidence interval; bold line, bottom of the 95% confidence interval. The bottom of the 95% confidence interval of *Cycladicama cumingi* extends across the lower sequence boundary. (1) Cold-water *Megangulus* Association.

block with the long side parallel to the strike of the stratum, 0.5 m in width and 2.0 m in length on average. The surfaces of the exposures were so uneven that the thickness of the block ranged from 0.05 to 0.5 m depending on the conditions of the section. For disarticulated shells, separated valves were counted and the totals were divided by two to determine the number of individuals. As mentioned above, the mixing of shells was restricted to a surface layer about 10 cm thick throughout deposition of the muddy sand yielding

warm-water species. Consequently, the accuracy of the chronological order of immigration of individuals is 10 cm in thickness.

In the present study, the following three sequences have been excluded for the following reasons: (1) within depositional sequence 4, no warm-water species occur except for *Stellaria exutum*; (2) in depositional sequence 7, all of the warm-water species excluding *Paphia schnelliana* are found in no more than a single horizon within the sequence; and (3) since depositional sequence

Horizons	molluscan association	<i>Paphia schnelli</i>	<i>Stellaria exutum</i>	<i>Zeuxis castus</i>	<i>Cycladicama cumingi</i>	<i>Jupiteria gordonis</i>	<i>Crenulimopsis oblonga</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
7.3-7.55	warm-water <i>Stellaria-Paphia</i> Association	1	0	0	0	1	1	13	HST
7.05-7.3		0	2	0	0	0	1	12	
6.8-7.05		1	3	0	0	2	2	13	
6.55-6.8		1	3	0	0	2	0	14	
6.3-6.55		1	2	0	0	1	3	11	
5.9-6.3		2	3	0	0	1	5	31	
5.5-5.9		1	2	0	0	0	8	24	
5.25-5.5		1	0	0	0	1	8	24	
5.0-5.25		3	3	0	0	1	2	18	
4.75-5.0		1	1	0	0	4	1	30	
4.5-4.75		1	6	0	0	1	3	24	
4.25-4.5		2	4	0	0	2	0 ↓ ₅₀	20	
4.0-4.25		0	0	0	0	1	0 ↓ ₈₀	3	
3.75-4.0		0	1	0	0	1	0	3	
3.5-3.75	0	1	0	0	2	0	2		
3.25-3.5	2	1	0	0	2	0	7		
3.0-3.25	2	3	0	0	1	0	10		
2.75-3.0	0	4	0	0	3	0	16		
2.5-2.75	1	1	0	0	3	0	11		
2.25-2.5	0	1	0	0	0	0	4		
2.0-2.25	2	1	0	0	0	0	6		
1.75-2.0	2	1	0	0	1	0	6		
1.55-1.75	1	1	1	1	0	0	6		
1.4-1.55	0	1	3	1	0 ↓ ₅₀	0 ↓ ₉₅	5		
1.25-1.4	1	0	1	0	0	0	2		
1.05-1.25	0	0	0 ↓ ₅₀	0	0	0	5		
0.75-1.05	0	0 ↓ ₅₀	0	0 ↓ ₅₀	0	0	6		
0.5-0.75	0	0	0	0	0 ↓ ₈₀	0	1		
0.25-0.5	0 ↓ ₅₀	0	0	0	0	0	2		
0.0-0.25	0	0	0 ↓ ₈₀	0	0	0	3		
	Clinocardium-Turritella Association								TST

Fig. 4. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 2 of the Omma Formation. See legend in Fig. 3.

8 has been assigned to two obliquity cycles (Shackleton et al., 1990), the stratigraphic distribution of warm-water species in this sequence is considered to be too complex for the analytical approach.

4. Results

In the present study, we focus on the six species among significant warm-water species in the middle part of the Omma Formation, because their

Horizons	molluscan association	<i>Paphia schnelli</i>	<i>Stellaria exutum</i>	<i>Zeuxis castus</i>	<i>Jupiteria gordonis</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
3.4-3.9	<i>Stellaria-Paphia</i> Association	4	6	0	0	30	TST
3.0-3.4		3	2	0	0	8	
2.8-3.0		2	5	0	0	12	
2.6-2.8		3	1	1	1	13	
2.3-2.6		1	2	1	1	12	
1.9-2.3		1	5	6	0	21	
1.5-1.9	0 ↓ ₅₀	5	4	0 ↓ ₅₀	22		
1.25-1.5	0 ↓ ₈₀	5	0	0	7		
1.0-1.25	0	4	0	0	10		
0.9-1.0	0	0	0 ↓ ₅₀	0	7		
0.5-0.9	0 ↓ ₉₅	0 ↓ ₅₀	0 ↓ ₈₀	0	42		
0.0-0.5	(1)	0	0 ↓ _{80,95}	0 ↓ ₉₅	0 ↓ ₈₀	51	

Fig. 5. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 3 of the Omma Formation. (1) *Felaniella* Association. See legend in Fig. 3.

Horizons	molluscan association	<i>Paphia schnelliana</i>	<i>Stellaria exutum</i>	<i>Zeuxis castus</i>	<i>Cycladicama cumingi</i>	<i>Crenulimopsis oblonga</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
3.75-3.85	(1)	0	1	0	0	2	19	TST
3.65-3.75	Stellaria - Paphia I Association	0	2	4	1	2	15	
3.55-3.65		1	1	1	1	4	16	
3.45-3.55		0	5	1	0	2	12	
3.35-3.45		0	1	1	0	1	10	
3.25-3.35		0	1	4	0	0	7	
3.15-3.25		1	2	0	0 ↓ ₅₀	0	8	
3.05-3.15	Clinocardium - Turritella Association	0	1	0	0	2	11	
2.9-3.05		0	1	1	0	0	11	
2.75-2.9		0	1	0	0	0 ↓ ₅₀	9	
2.6-2.75		0	0	0 ↓ ₅₀	0	0	6	
2.1-2.6		0 ↓ ₅₀	0 ↓ ₅₀	0	0	0 ↓ ₈₀	14	
1.6-2.1		0	0 ↓ ₈₀	0 ↓ ₈₀	0	0	9	
1.1-1.6	0	0	0	0	0	3		
0.7-1.1	0	0	0	0	0	2		
0.3-0.7	0	0	0	0	0	7		
0.0-0.3	0	0	0	0	0	2		

Fig. 6. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 5 of the Omma Formation. (1) *Clinocardium-Turritella* Association. See legend in Fig. 3.

confidence intervals were successfully determined in more than three depositional sequences. All of them are extant species on the shelf around Japan (Kitamura et al., 1994). The 50%, 80% and 95% confidence intervals for them within each depositional sequence are shown in Figs. 3–9. Most of the 95% confidence intervals extend across the

lower sequence boundary. Within each depositional sequence, molluscan fossils are rare in the horizon represented by the cold-water *Clinocardium-Turritella* Association, compared with the horizon yielding warm-water species. The significant difference of fossil abundance among horizons reflects the difference of the rate of sedimentation

Table 1
Water temperature conditions in the northern limits of the six selected warm-water species

Species	Common habitat depth (m)	Northern limit	Bathymetric range in northern limit (m)	Minimum and maximum bottom water temperatures in northern limit	References
<i>Zeuxis castus</i>	10–200	Otsuchi Bay at the northern Sanriku coast	20–70	6°C and 16–20°C at 20–70 m deep	Tsuchida (1991)
<i>Cycladicama cumingi</i>	10–50	northern Sanriku coast	10–200	6°C and 16–20°C at 20–70 m deep	Ishiyama (1973)
<i>Paphia schnelliana</i>	10–100	Otsuchi Bay at the northern Sanriku coast	90	6°C and 16–20°C at 20–70 m deep	Tsuchida and Kurozumi (1996)
<i>Crenulimopsis oblonga</i>	50–200	Otsuchi Bay at the northern Sanriku coast	50–150	6°C and 16–20°C at 20–70 m deep	Tsuchida and Kurozumi (1993)
<i>Stellaria exutum</i>	20–350	off the Oga peninsula	20–40	9°C and 20–23°C at 30 m deep	Higo and Goto (1993), Higo et al. (1999)
<i>Jupiteria gordonis</i>	20–200	off northern Niigata area	20–100	9–10°C and 15°C at 100 m deep	Takayasu and Yunohara (1977), Ito et al. (1986), Ito (1989), Tsuchida and Hayashi (1994)

Horizons	molluscan association	<i>Paphia schnelliana</i>	<i>Stellaria exutum</i>	<i>Zeuxis castus</i>	<i>Cycladicama cumingi</i>	<i>Crenulilimopsis oblonga</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
7.9-8.3	Clinocardium-Turritella Association	0	0	0	0	0	16	RST
7.8-7.9		0	0	0	0	0	16	
7.7-7.8		0	0	0	0	0	18	
7.6-7.7		0	0	0	0	0	18	
7.5-7.6		0	0	0	0	0	16	
7.3-7.5		0	0	0	0	0	35	
7.1-7.3		0	0	0	0	0	23	
6.8-7.1		0	0	0	0	0	18	
6.5-6.8		0	0	0	0	0	34	
6.2-6.5		0	0	0	0	0	55	
6.0-6.2		0	0	0	0	0	34	
5.8-6.0		0	0	0	0	0	36	
5.6-5.8		0	0	0	0	0	31	
5.4-5.6		0	0	0	0	0	29	
5.2-5.4		0	0	0	0	0	26	
5.0-5.2		0	0	0	0	0	16	
4.8-5.0		0	0	0	0	0	14	
4.6-4.8		0	0	0	0	0	9	
4.3-4.6		0	0	0	0	0	23	
4.0-4.3		0	0	0	0	1	25	
3.7-4.0	0	0	0	0	1	17		
3.4-3.7	0	0	0	0	0	40		
3.1-3.4	0	0	0	0	6	27		
2.9-3.1	1	2	1	0	5	58		
2.7-2.9	9	5	5	2	4	57		
2.5-2.7	1	3	2	0	2	31		
2.3-2.5	2	3	2	0	3	27		
2.1-2.3	2	3	2	1	1	15		
1.9-2.1	2	6	0	0	2	24		
1.7-1.9	2	2	0	0	1	7		
1.5-1.7	2	2	0	0	0	16		
1.3-1.5	1	2	1	0	0	19		
1.1-1.3	0	0	0	0	0 ↓ ₅₀	7		
0.9-1.1	(2)	0	0	0	0	8		
0.5-0.9	0 ↓ ₅₀	0 ↓ ₅₀	0	0	0 ↓ ₈₀	10		
0.0-0.5	(1)	0 ↓ ₈₀	0 ↓ ₈₀	0 ↓ ₅₀	0	30		

Fig. 7. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 6 of the Omma Formation. (1) *Felaniella* Association, (2) *Clinocardium-Turritella* Association. See legend in Fig. 3.

between the early and late transgressive phases (Kondo et al., 1998). In the present analysis, low abundances of cold-water species resulted in considerably wide confidence intervals, especially at the 95% level.

In any depositional sequence, the bottom of the 50% confidence interval of *Jupiteria gordonis* is stratigraphically situated above the base of the observed range of *Paphia schnelliana* (except for sequence 3), *Stellaria exutum*, *Zeuxis castus* and *Cycladicama cumingi* (Figs. 4, 5, 8 and 9). In depositional sequence 10, the bottom of the 80% confidence interval of *J. gordonis* is much higher than that of the observed range of *P. schnelliana* and *C. cumingi* (Fig. 8). In depositional sequence

2, the bottom of the 80% confidence interval of *Crenulilimopsis oblonga* is located above the base of the observed range of *S. exutum* and *Z. castus* (Fig. 8). These results clearly show that, in immigration events during climate warming, *J. gordonis* tended to lag behind *P. schnelliana*, *S. exutum*, *Z. castus* and *C. cumingi*, while *S. exutum* and *Z. castus* heralded the coming of *C. oblonga*.

5. Discussion and conclusions

As far as the above-mentioned six species are concerned, there is no evidence that ecological factors, such as competition or predation, restrict

Horizons	molluscan association	<i>Paphia schnelliana</i>	<i>Cycladicama cumingi</i>	<i>Jupiteria gordonis</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation	
7.0-7.2	(2)	0	0	5	55	HST	
6.8-7.0	Climocardium-Turritella Association	0	0	7	13		
6.6-6.8		1	0	6	20		
6.4-6.6		0	0	9	20		
6.2-6.4		0	0	7	20		
6.0-6.2		2	0	13	23		
5.8-6.0	Stellaria-Paphia II Association	2	0	18	28		
5.6-5.8		1	3	18	29		
5.4-5.6	warm-water Cycladicama Association	0	4	15	30		TST
5.2-5.4		1	10	3	20		
5.0-5.2		0	6	1	11		
4.8-5.0		0	1	0	3		
4.6-4.8		0	5	0	7		
4.4-4.6		0	4	0 ↓ ₅₀	6		
4.2-4.4		0	6	0	7		
4.0-4.2		0	2	0	3		
3.8-4.0		0	3	0 ↓ ₈₀	3		
3.6-3.8		0	2	0	2		
3.4-3.6	0	3	0	3			
3.2-3.4	0	1	0	1			
3.0-3.2	1	3	0	4			
2.8-3.0	0	0	0	0			
2.6-2.8	0	0	0	1			
2.4-2.6	0	3	0	3			
2.2-2.4	0	1	0	1			
2.0-2.2	0	0	0	0			
1.8-2.0	(1)	0	0	0	2		
1.6-1.8	0	0	0	0			
1.4-1.6	Climocardium-Turritella Association	0	0	0	4		
1.2-1.4		0	0 ↓ ₅₀	0	10		
1.0-1.2		0	0 ↓ ₈₀	0	13		
0.8-1.0		0	0 ↓ ₉₅	0	20		
0.6-0.8		0 ↓ ₅₀	0	0 ↓ ₉₅	17		
0.4-0.6	Felaniella Association	0	0	0	19		
0.2-0.4		0 ↓ ₈₀	0	0	46		
0.0-0.2		0	0	0	30		

Fig. 8. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 10 of the Omma Formation. (1) An interval barren of molluscs (Kitamura et al., 2000b), (2) *Felaniella* Association. See legend in Fig. 3.

the geographic distribution of these species. In addition, some of the six species often co-occur with each other and with other species within a single stratigraphic horizon in the Omma Formation (Kitamura, 1991). For these reasons, we believe that neither competition nor predation is a major factor controlling the timing of immigration of each species with climatic change. Comparison of the stratigraphic order of the first appearance of the six species with the modern geographic distribution relies on the assumption that tolerance of these species to environmental change has not significantly changed throughout the Quaternary period. Consequently, data on the modern geographic distribution of the six species provide a reliable constraint on modeling the mi-

gration of offshore molluscs during a climatic warming phase (Table 1).

The first appearance of *Jupiteria gordonis* within a sequence tends to be later than other significant species. Based on the northern limits of geographic distribution and bathymetric ranges at present, *J. gordonis* appears to have a lower tolerance to a low temperature than other species. This fact explains well why its immigration is so late during a warming climate phase. On the other hand, *Crenulilimopsis oblonga* lives particularly in deeper water among the six species. Thus, its bathymetric range and/or dispersal capability of larvae may be the reasons for the relatively later immigration of *C. oblonga* during a deglacial warming climate phase.

Horizons	molluscan association	<i>Paphia schnelliana</i>	<i>Cycladicama cumingi</i>	<i>Jupiteria gordonis</i>	Total numbers of molluscan fossils	sequence stratigraphic interpretation
7.38-7.68	Cinocardium-Turritella Association	0	0	0	17	RST
6.98-7.38		0	0	0	35	
6.58-6.98		0	0	0	13	
6.18-6.58		0	0	0	6	
5.78-6.18		0	0	0	32	
5.68-5.78		0	0	0	3	
5.58-5.68		0	0	0	5	
5.48-5.58		0	0	0	15	
5.28-5.48		0	0	0	88	
5.13-5.28		0	0	0	15	
5.03-5.13		0	0	0	38	
4.93-5.03		0	0	0	27	
4.63-4.93		0	0	0	33	
4.53-4.63		0	0	0	16	
4.43-4.53		0	0	0	9	
4.33-4.43		0	0	0	7	
4.23-4.33		0	0	0	13	
4.13-4.23		0	0	0	9	
4.03-4.13		0	0	0	11	
3.93-4.03		0	0	0	9	
3.83-3.93		0	0	0	13	
3.68-3.83		0	0	0	15	
3.58-3.68		0	0	3	23	
3.43-3.58		1	11	1	26	
3.33-3.43		1	15	1	21	
3.18-3.33		0	19	0	30	
3.08-3.18	0	6	0 ↓ ₅₀	22		
2.98-3.08	2	10	0	28		
2.88-2.98	0	4	0	9		
2.78-2.88	1	0	0	16		
2.68-2.78	0	0	0	7		
2.58-2.68	0	0 ↓ ₅₀	0	9		
2.48-2.58	0	0	0	8		
2.38-2.48	0	0	0	3		
2.28-2.38	0	0 ↓ ₈₀	0	6		
2.13-2.28	0 ↓ ₅₀	0	0	8		
2.05-2.13	0	0	0	20		
1.9-2.05	0	0	0	22		
1.6-1.9	0 ↓ ₈₀	0 ↓ ₉₅	0 ↓ ₈₀	16		
1.53-1.60	0	0	0	3		
1.45-1.53	0	0	0	12		
1.35-1.45	0	0	0	17		
1.3-1.35	0	0	0	8		
1.1-1.3	0	0	0	7		
1.05-1.1	0	0	0	6		
0.9-1.05	0	0	0	15		
0.8-0.9	0	0	0	15		
0.4-0.8	0	0	0	6		
0.3-0.4	0	0	0	24		
0.2-0.3	0	0	0	8		
0.1-0.2	0	0	0	8		
0.0-0.1	0	0	0	25		
	Cycladicama Association					HST
	Cinocardium-Turritella Association					TST
	Faunella Association					

Fig. 9. The 50%, 80% and 95% confidence intervals for selected warm-water species within depositional sequence 11 of the Omma Formation. See legend in Fig. 3.

Because the modern northern limit of distribution of *Stellaria exutum* is more restricted than that of *Paphia schnelliana*, *Zeuxis castus*, *Cycladicama cumingi* and *Crenulilimopsis oblonga*, its immigration would be expected to follow them. Nevertheless, significant differences are not found in the timing of immigration between *S. exutum* and the latter four species. In the present study, there are no data on the environmental change

itself during deglaciations and its influences on the manner of migration of warm-water species. Thus, the reason for the unexpectedly early immigration of *S. exutum* is still uncertain. A possible answer to this question may lie in the high dispersal capability of its larval stage. If so, absence of the significant species except for *S. exutum* in depositional sequence 4 may imply that the warming during transition from oxygen isotope stages

44 to 43 was so rapid that these warm-water species could not spread their geographic distributions because of their low dispersal capability.

Analyses of fossil shallow-marine molluscs of the early Pleistocene Omma Formation demonstrate that the chronological order of immigration of the warm-water species was not always consistent with their modern geographic distributions. This inconsistency may be caused by differences in dispersal capability among the species. Therefore detailed information on larval ecology as well as physiological tolerances is necessary to determine how marine molluscs respond to rapid climatic warming. The approach in this study is useful for addressing the issue.

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