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Water temperature, salinity ranges and ecological significance of the three families of Recent cold-water ostracods in and around the Japan Sea

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Abstract. Water temperature (T) and salinity (S) ranges for the modern distribution of relict species of cold-water ostracods in and around the Japan Sea are summarized. These results provide new information on the ecology of species in the Omma-Manganji ostracod fauna and their survival through Pleistocene environmental changes. Fourteen representative species of this fauna belonging to the three families Hemicytheridae, Cytheruridae and Eucytheridae are discussed. The summer T-S habitat requirements were divided into three species groups: (a) Japan open sea-inner bay (0–20˚C, 30–34‰; 9 species); (b) Japan-Alaska open sea (around 5˚C, 31–34‰; 1 species); (c) Japan open sea (0–20˚C, around 34‰; 4 species). The winter T-S of these three species groups falls in a single range of 0–5˚C and 30–34‰. Their summer T-S conditions are characterized by a wide range either for T or S or both. The summer T range of most species reflects the Tsushima Warm Current water in summer. The winter T range of all the species corresponds to the coldest Japan Sea Intermediate-Proper Water through the year. The large T range difference between summer and winter is a remarkable character of most species. It is clear that most of these species examined here also live in temperatures as high as 20˚C, but are generally cold-water species as a whole. The winter low T (less than 5˚C) is considered to be critical for the survival of all of these species. These species were interpreted as having survived the cyclic environmental changes between glacial and interglacial periods by expansion or contraction of their distribution. Group (a) species can inhabit various T-S environments in summer. Furthermore, they can probably breed and maintain their populations, even in small areas such as the restricted inner bay, when suitable open sea conditions were lost. Group (b) species have only recently migrated to the low T-S region in the Northeast Pacific, and low T regions of deeper areas of the eastern Japan Sea where only a few species live. Group (c) species invaded the newly appearing T-S condition in the shallow-open areas of the Japan Sea, and have flourished, replacing the extinct species during the Pleistocene. Their wide T-S tolerance is considered to be the most advantageous factor for survival through the Pleistocene environmental fluctuations in the Japan Sea, linked with the glacio-eustatic sea-level changes.

Key words: cold-water ostracods, ecology, Japan Sea, Omma-Manganji fauna, Recent, relict species, water temperature-salinity range

Introduction

Recognizing the responses of the world's ecosystems to Quaternary climate oscillation provides key insights for modeling potential future human-induced climatic changes on the world's biotas (e.g. Cronin, 1999; Cronin *et al.*, 1999). Thus, investigations of past faunas, for example, of the migration, extinction and survival of cryophilic species, in response to climatic warming events, have become increasingly important. The Japan Sea and its fauna are particularly suitable for investigations of the biotic responses to the oceanic environmental changes during the Quaternary. This is due to the fact that the region is a typical semi-closed marginal sea, located at middle latitudes where the oceanic conditions change in response to the glacio-

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eustatic sea-level fluctuations associated with climatic oscillations (e.g. Oba *et al.*, 1991; Ikehara, 1998). Furthermore, various faunas live in the shallow sea in several types of water masses (e.g. Nishimura, 1966; Tsuchida and Hayashi, 1994). However, there are few studies which discuss survival and extinction in terms of water mass properties in both Recent and geological times with specific water temperature and salinity characteristics. Benthic Ostracoda (Crustacea) are good subjects for this work, because they are abundant in both Quaternary strata and in Recent samples, unlike many other organisms (e.g. Okada, 1979; Irizuki, 1993; Ozawa and Kamiya, 2001). Furthermore, many species live in particular types of water masses (e.g. Ishizaki and Irizuki, 1990; Ikeya and Suzuki, 1992; Ozawa, 1998, 2003a).

In this study, we examined survival factors of cold-water ostracods in representative families of the Omma-Manganji ostracods in and around the Japan Sea, in terms of the relationship with oceanic environmental changes during the Quaternary. These ostracods are the characteristic fauna in the Pliocene and Pleistocene Japan Sea, and are characterized by high-species diversity (e.g. Cronin and Ikeya, 1987; Ozawa, 1996). The term ''Omma-Manganji fauna'' was originally applied to the cold-water molluscan assemblages from the Pliocene on the Japanese Islands, named after the outcrop areas in central and northeastern Japan (e.g. Otuka, 1939; Chinzei, 1978). The term Omma-Manganji ostracod fauna was first published by Cronin and Ikeya (1987), and included ca. 50 species. However, the definition of this fauna by Cronin and Ikeya (1987) is not clear. These are so-called cold-water or cold-current species (e.g. Okada, 1979), because they belong to genera that inhabit higher latitudes than the Japan Sea today (e.g. Tabuki, 1986). These ostracods commonly occur in the Pliocene and Pleistocene shallow-marine strata along the Japan Sea coast. Therefore, these species are considered to flourish in the cold-water environment in the shallow sea especially during glacial periods. After that, due to the repeated warm-current inflow during Pleistocene interglacial periods (e.g. Tada, 1994; Kitamura *et al.*, 1994; Ozawa and Kamiya, 2001), it had been inferred that many of these cold-water species are now extinct at least around the Japanese Islands (Ozawa, 2001).

However, living specimens of the cold-water species in representative families in this fauna, Hemicytheridae, Cytheruridae and Eucytheridae, were recovered from the northern Japan Sea in the 1990's, by offshore investigations (e.g. Itoh, 1996a; Ozawa *et al.*, 1999; Tsukawaki *et al.*, 1999). As a result, these ostracods are now regarded as relict species (e.g. Ozawa, 1998, 2003b). We can now study their ecology such as water temperature and salinity, because the characters of living environment for these species are still not understood.

Since the 1990's, it has been established that some of these species in the three families, especially the Hemicytheridae, were misidentified and the juvenile-adult relationship of some species was unrecognized by some workers. This led to new genera and species being described (e.g. Hanai and Ikeya, 1991; Irizuki, 1993, 1996a). In recent studies, many species have assigned to different genera and have different species names from studies before the 1990's.

The first aim of this study is to reexamine and summarize the Recent geographical and water depth distributions of the cold-water ostracods in three families in and around the Japan Sea. The second aim is to identify the specific ranges of water temperature and salinity in their distributional areas in summer and winter. The goal of this study is to understand the survival factors for the cold-water species in the marginal sea through the Quaternary environmental changes, in terms of the water mass conditions. Furthermore, the so-called cold-water environment in their habitats and in shallow-sea areas of the Japan Sea during glacial periods are reexamined.

Analytical methods

This study focuses on 14 representative species of cold-water ostracods, especially in the three families: Hemicytheridae, Cytheruridae and Eucytheridae (Figure 1). The Recent distribution of these 14 species is summarized below. These 14 species were chosen because they abundantly occur from the Pliocene and Pleistocene strata along the Japan Sea coast with the Omma-Manganji molluscan fossils and are representative species commonly found from many strata. Furthermore, they are relatively easy to identify, so that the results may be compared with previous studies, which contained only species lists and no illustrations.

In order to summarize the Recent geographical and water depth distributions of the 14 species, the published data from the Japan Sea coast were checked (Ishizaki, 1969, 1971; Irizuki, 1989a; Takayasu *et al.*, 1990; Ikeya and Suzuki, 1992; Tsukawaki *et al.*, 1993, 1997, 1998, 1999, 2000; Kamiya *et al.*, 1997, 2001; Tanaka *et al.*, 1998; Ozawa *et al.*, 1999; Schornikov, 2000). Furthermore, species occurrences from other seas were summarized from the following literature: Ishizaki, 1968, 1981; Schornikov, 1974; Okubo, 1980;

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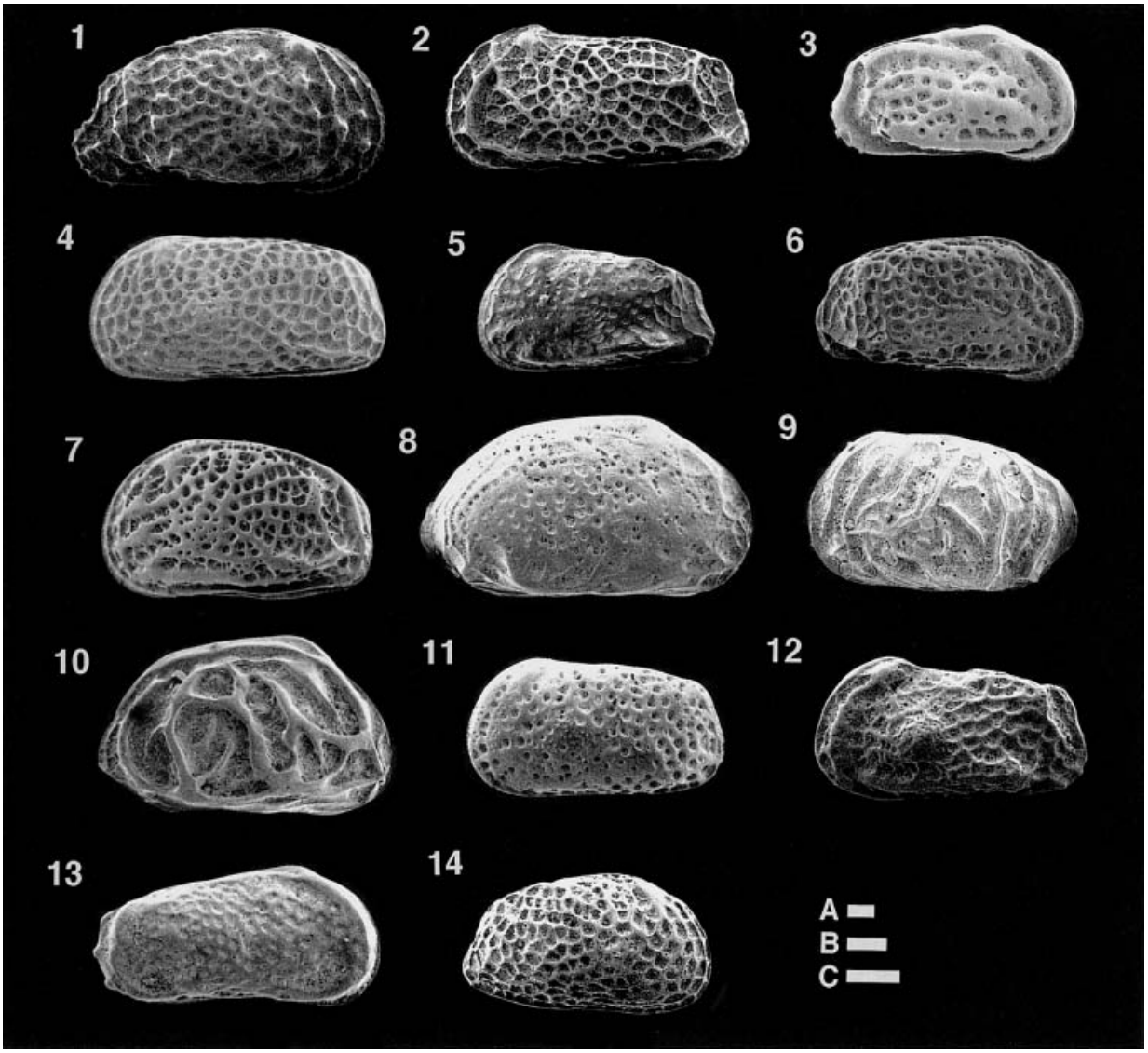


Figure 1. The fourteen species of Recent cold-water ostracods examined in this study. **1**. *Baffinicythere ishizakii* Irizuki, RV. **2**. *Baffinicythere robusticostata* Irizuki, LV. **3**. *Cornucoquimba alata* Tabuki, RV. **4**. *Daishakacythere abei* (Tabuki), LV. **5**. *Daishakacythere posterocostata* (Tabuki), LV. **6**. *Finmarchinella nealei* Okada, RV. **7**. *Hemicythere orientalis* Schornikov, LV. **8**. *Howeina camptocytheroidea* Hanai, RV. **9**. *Howeina higashimeyaensis* Ishizaki, LV. **10**. *Howeina leptocytheroidea* (Hanai), RV. **11**. *Johnnealella nopporensis* Hanai and Ikeya, LV. **12**. *Laperousecythere robusta* (Tabuki), LV. **13**. *Munseyella hatatatensis* Ishizaki, RV. **14**. *Yezocythere hayashii* Hanai and Ikeya, RV. Specimens of figs. 1–7, 11, 12, 14: family Hemicytheridae; 8–10: Cytheruridae; 14: Eucytheridae. All specimens are adult valves, except for the specimen in fig. 5 (juvenile valve). 1, 2, 8, 11, 12, 13, 14 from off Abashiri, Okhotsk Sea; 3 from Akkeshi Bay; 4–7, 9, 10 from off Teuri Island, Japan Sea. Scale bars are 0.1 mm (A for 1–5, 11, 12, 14; B for 6, 7; C for 8–10, 13). LV: left valve, RV: right valve.

Frydl, 1982; Ikeya and Hanai, 1982; Abe, 1983; Ikeya *et al.*, 1985, 1992; Bodergat and Ikeya, 1988; Brouwers, 1990, 1993; Ikeya and Itoh, 1991; Iwasaki, 1992; Ikeya and Cronin, 1993; Zhou, 1995; Itoh, 1996b, 1998; Zhou *et al.*, 1996; Yamane, 1998; Yasuhara and Irizuki, 2001; Nakao *et al.*, 2001; Nakao and Tsukagoshi, 2002. Species occurrences from bottom sediment samples around Hokkaido, from Akkeshi Bay, off Abashiri, Kushiro and Rebun Island areas were added by this study (Table 1).

Among the previously published reports, the distributional records suspected to be reworked fossil specimens from Pleistocene strata, based on their poor preservation as indicated by Irizuki (1996a) etc., were excluded here. These reports are from Sendai Bay (Ikeya and Itoh, 1991), around the Noto Peninsula

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Table 1. Sample localities for Recent 14 species from four areas around Hokkaido. Detailed locations of samples from Off Abashiri and Off Kushiro are described in Tsukawaki *et al.* (2003) and Tsukawaki and Nemoto (1991), respectively. Species names; Bai: *Baffinicythere ishizakii*, Bar: *Baffinicythere robusticostata*, Coa: *Cornucoquimba alata*, Daa: *Daishakacythere abei*, Dap: *Daishakacythere posterocostata*, Fin: *Finmarchinella nealei*, Heo: *Hemicythere orientalis*, Hoc: *Howeina camptocytheroidea*, Hoh: *Howeina higashimeyaensis*, Hol: *Howeina leptocytheroidea*, Jon: *Johnnealella nopporensis*, Lar: *Laperousecythere robusta*, Muh: *Munseyella hatatatensis*, Yeh: *Yezocythere hayashii*.

Sample	Latitude (N)	Longitude (E)	Depth (m)	Species occurrence
Off Rebun Island				
R12	45°32.3′	141°16.5′	131	Muh
R11	45°29.3′	141°13.4′	130	Muh
R9	45°23.5′	141°09.8′	110	Muh
R8	45°21.7′	141°08.8′	100	Daa, Fin, Lar, Muh
R7	45°20.3′	141°08.0′	90	Bar, Hoh, Lar
R6	45°18.0′	141°07.1′	80	Bar, Daa, Heo, Jon, Lar
R5	45°18.0′	141°05.8′	75	Bai, Bar, Coa, Daa, Dap, Fin, Heo, Hoh, Hol, Jon, Lar, Yeh
R4	45°18.0′	141°04.6′	60	Bai, Bar, Daa, Fin, Hoh, Hol, Jon, Muh, Yeh
R3	45°18.0′	141°04.3′	50	Daa, Fin, Hoh, Hol, Jon, Yeh
R2	45°18.0′	141°03.7′	20	Daa, Fin, Hol
R13	45°13.7′	141°03.6′	80	Bai, Bar, Daa, Dap, Fin, Jon, Lar, Muh
R14	45°12.3′	141°02.1′	100	Bai, Daa, Fin, Jon, Lar
Off Abashiri (KT01-14 Cruise)				
G12	44°08.2′	144°38.7′	493	Bai, Lar, Muh
G11	44°07.8′	144°38.9′	423	Jon, Lar, Muh
G10	44°06.2′	144°38.0′	250	Bar, Coa, Lar, Muh
G9	44°04.9′	144°37.2′	193	Bar, Coa, Jon, Lar, Muh
G8	44°04.6′	144°37.1′	174	Bai, Bar, Coa, Fin, Heo, Hoc, Jon, Lar, Muh
G7	44°04.4′	144°36.9′	142	Bar, Coa, Fin, Jon, Lar, Muh
G6	43°03.6′	144°37.2′	117	Bai, Bar, Coa, Fin, Hoc, Jon, Lar, Muh
G5	44°02.9′	144°37.5′	99	Bai, Bar, Coa, Fin, Hoc, Jon, Lar, Muh
G4	44°01.2′	144°37.2′	72	Bai, Bar, Coa, Fin, Hoc, Jon, Lar, Muh, Yeh
G3	43°58.0′	144°34.7′	49	Fin, Jon
Akkeshi Bay				
M2	43°02.0′	144°49.5′	7	Coa, Heo, Hoc, Muh, Yeh
IT33	43°01.9′	144°51.9′	1	Fin, Heo
IT24	43°01.3′	144°50.2′	10	Coa, Heo, Hoc, Hol, Muh, Yeh
M6	43°00.0′	144°51.5′	1	Coa, Heo, Hoc, Muh, Yeh
IT5	43°00.0′	144°45.0′	4	Coa, Heo, Hoc, Hol, Muh, Yeh
IT16	42°59.9′	144°50.2′	16	Coa, Fin, Heo, Hoc, Jon, Muh, Yeh
IT15	42°58.4′	144°51.5′	20	Coa, Fin, Heo, Hol, Jon, Muh, Yeh
IT12	42°58.4′	144°47.5′	18	Coa, Fin, Hoc, Jon, Muh, Yeh
M10	42°58.0′	144°54.0′	14	Coa, Heo, Hoc, Hol, Jon, Muh, Yeh
IT6	42°57.0′	144°50.2′	30	Coa, Fin, Heo, Muh, Yeh
IT7	42°57.0′	144°48.9′	28	Coa, Fin, Hoc, Muh, Yeh
IT2	42°55.0′	144°52.1′	50	Coa, Heo, Hoc, Jon, Muh, Yeh
IT1	42°54.8′	144°52.1′	50	Coa, Fin, Jon, Muh, Yeh
Off Kushiro (KT90-9 Cruise)				
G16	42°48.0′	143°52.6′	16	Muh
G19	42°33.0′	143°55.2′	131	Yeh

(Irizuki, 1989a; Tsukawaki *et al.*, 1997) and around the Sado Island region (Tsukawaki *et al.*, 1993).

To establish the environmental factors of their distributional areas in summer and winter, the mean values of water temperature and salinity in August and February were used. Here, the temperature and salinity for the open-sea regions, the average data between 1906–1994 within one degree of latitude and longitude of each depth between 0–500 m (surface, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 400, 500 m) from the Japan Oceanographic Data Center (JODC) database (http://www.jodc.go.jp/service_j.htm) were utilized. The mean values at the nearest water depth for each site, summarized in this study, were used. Some areas lacking JODC data for the Alaska region were covered by Brouwers (1988). For the four inner bay regions in northern Japan, survey reports for the water temperature and salinity in each bay were used,

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in Otsuchi Bay (Terazaki and Shikama, 1979), Mutsu Bay (Nagamine *et al.*, 1982), Akkeshi Bay (Nakamura *et al.*, 1997) and Lake Saroma (Tada and Nishihama, 1988).

Results

Geographical distribution

The 14 species discussed here are distributed in the western, eastern and northern Japan Sea; the southern Okhotsk Sea off Hokkaido; and inner bay regions in northern Japan (Figure 2). Only one species is distributed in the northeast Pacific, and only one species is reported from the northern Yellow Sea (Huanghai Sea). Figure 3 tabulates the summary distribution for both dead shells and living specimens with soft parts, and their water depth ranges. In the Family Hemicytheridae, there are 10 species: *Baffinicythere ishizakii*, *B. robusticostata*, *Cornucoquimba alata*, *Daishakacythere abei*, *D. posterocostata*, *Finmarchinella nealei*, *Hemicythere orientalis*, *Johnnealella nopporensis*, *Laperousecythere robusta* and *Yezocythere hayashii*; three species in the Cytheruridae, *Howeina camptocytheroidea*, *H. higashimeyaensis* and *H. leptocytheroidea*; and one species in the Eucytheridae, *Munseyella hatatatensis* (Figure 1).

All 14 species occur in open-sea areas along the northern Japan Sea off Hokkaido Island. Eleven species were reported from the open-sea area in the southern Okhotsk Sea (Figure 3). Ten species occur in the four inner-bay areas in northern Japan along the Pacific and Okhotsk Seas. Among the four bay areas, a maximum of eight species were reported from Akkeshi Bay. Three species were found from the northwest Pacific region off Hokkaido Island. Only one species, *L. robusta*, occurs both around Japanese Islands and the northeast Pacific, Alaska area (ca. 58–61°N, 138–147°W; Brouwers, 1993). Only *H. camptocytheroidea* is distributed both around Japanese Islands and the northern Yellow Sea, east of Bohai

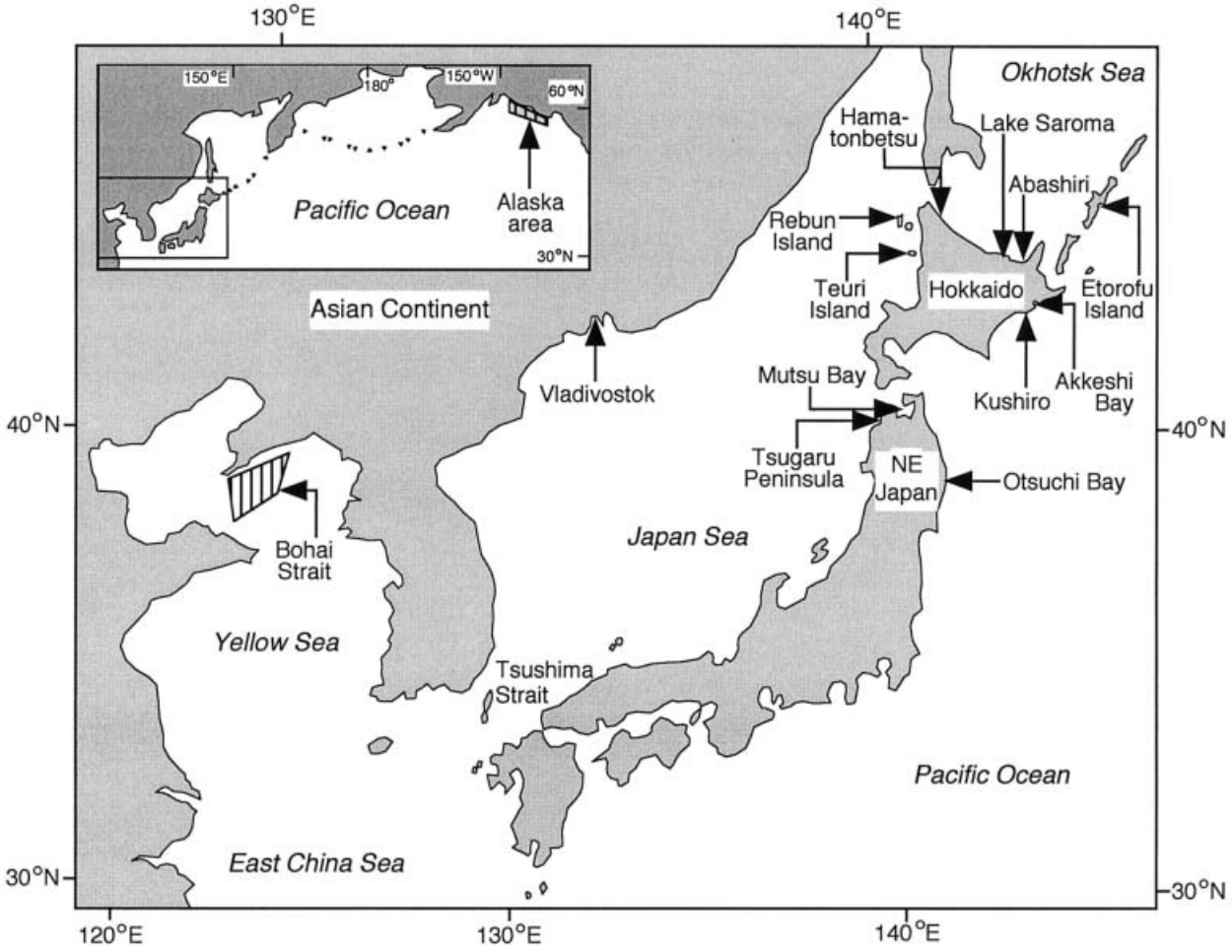


Figure 2. Index map showing the localities on Recent distributional areas of the examined species.

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Sea area	Japan Sea				Southern Okhotsk Sea	
Species name/ Region	Off Tsugaru Pe.	Off Teuri Is.	Off Rebun Is.	Off Vladivostok	Off Hmtb.	Off Abashiri
Baffinicythere ishizakii		124	60-100 (4)		55-95 (5)	72-493 (7)
Baffinicythere robusticostata		60-124 (3)	60-90 (5)		15-106 (11)	72-250 (7)
Cornucoquimba alata		60	75		47-106 (10)	72-250 (7)
Daishakacythere abei		37-66 (4)	20-100 (8)			
Daishakacythere posterocostata		60-66 (2)	75-80 (2)			
Finmarchinella nealei		37-66 (4) [37]#	20-100 (7)		15-95 (5)	49-174 (6) [49]#
Hemicythere orientaris		37-66 (3) [37-43]#	75-80 (2)	(no depth data)		174
Howeina camptocytheroidea		37		(no depth data)	30-67 (3)	72-174 (4)
Howeina higashimeyaensis		37-67 (3)	50-90 (4)		15-106 (5)	
Howeina leptocytheroidea		60-66 (2)	20-75 (4)			
Johnnealella nopporensis		43-124 (3)	50-100 (6) [80]#		15-106 (11)	49-423 (8) [193]#
Laperousecythere robusta	153-190 (2) [190]#	66-124 (2) [66]#	75-100 (6) [80-100]#		15-106 (11)	72-493 (9) [99]#
Munseyella hatatatensis		37-124 (9) [39-70]#	60-131 (6)		15-106 (10)	72-493 (9) [117-423]#
Yezocythere hayashii		37-60 (3) [37]#	50-75 (3)	(no depth data)	15-106 (5)	72
Literature cited	(a)	(b)	(c)	(d)	(e)	(c)

Sea area	Inner bay in Northern Japan				Northwestern Pacific		NE. Pacific	N. Yellow Sea
Species name/ Region	Otsuchi	Mutsu	Akkeshi	Saroma	Off Ksr.	Off Etorofu Is.	Alaska	E. Bohai Strait
Baffinicythere ishizakii								
Baffinicythere robusticostata	30-90 (20)							
Cornucoquimba alata	70-90 (3)		1-50 (12) [1-10]#					
Daishakacythere abei								
Daishakacythere posterocostata								
Finmarchinella nealei			1-50 (7)					
Hemicythere orientaris		14-26 (8)	1-50 (10)			40-78 (2) [40]#		
Howeina camptocytheroidea		11-50 (23)	4-50 (9)	4-16 (20)				20-50 (9)
Howeina higashimeyaensis	10-90 (10)	16		8-12 (2)				
Howeina leptocytheroidea			4-20 (4)					
Johnnealella nopporensis			14-50 (6)	8-13 (2)				
Laperousecythere robusta							50-220 (36) [50-80]#	
Munseyella hatatatensis	10-90 (14)	41-50 (2)	1-50 (12)		16			
Yezocythere hayashii		11-52 (23)	1-50 (12) [12]#		131			
Literature cited	(f)	(g)	(c)	(h)	(c)	(i)	(j)	(k)

Figure 3. Summary of the Recent geographical occurrence and water depth range of the examined species. Number in the parenthesis means the number of samples within the water depth range. Number in the square bracket with # means the water depth or water depth range for the living specimens. Areal names; Pe.: Peninsula, Is.: Island, Hmtb.: Hamatonbetsu, NE.: Northeast, N.: Northern, Ksr.: Kushiro, E.: East of. Data are cited from (a) Tsukawaki *et al.* (1999), (b) Ozawa *et al.* (1999), (c) this study, (d) Schornikov (2000), (e) Ikeya and Cronin (1993), (f) Ikeya *et al.* (1992), (g) Ishizaki (1971), (h) Itoh (1996b), (i) Schornikov (1974), (j) Brouwers (1993), (k) Zhou *et al.* (1996).

Strait (ca. 38–39°N, 121–123°E; Zhou *et al.*, 1996). These 14 species distributions represent two species types: one that lives in the open sea and one that lives in both the open sea and inner bays.

This study deals with the data of modern ostracod distribution, which consist mostly of dead specimens without soft parts in bottom surface sediments (Figure 3). Then, this study essentially discusses the relationship between the water temperature-salinity properties and the distribution of the modern dead ostracods. Strictly speaking, in the surface sediments the places at which dead ostracod specimens occur are different from those of living animals, as a result of postmortem transportation of empty carapaces to some extent (e.g., Frydl, 1982; Irizuki *et al.*, 1999). However, distinguishing between the autochthonous and allochthonous shells of ostracods is very difficult, and it is nearly impossible to estimate the postmortem-transported

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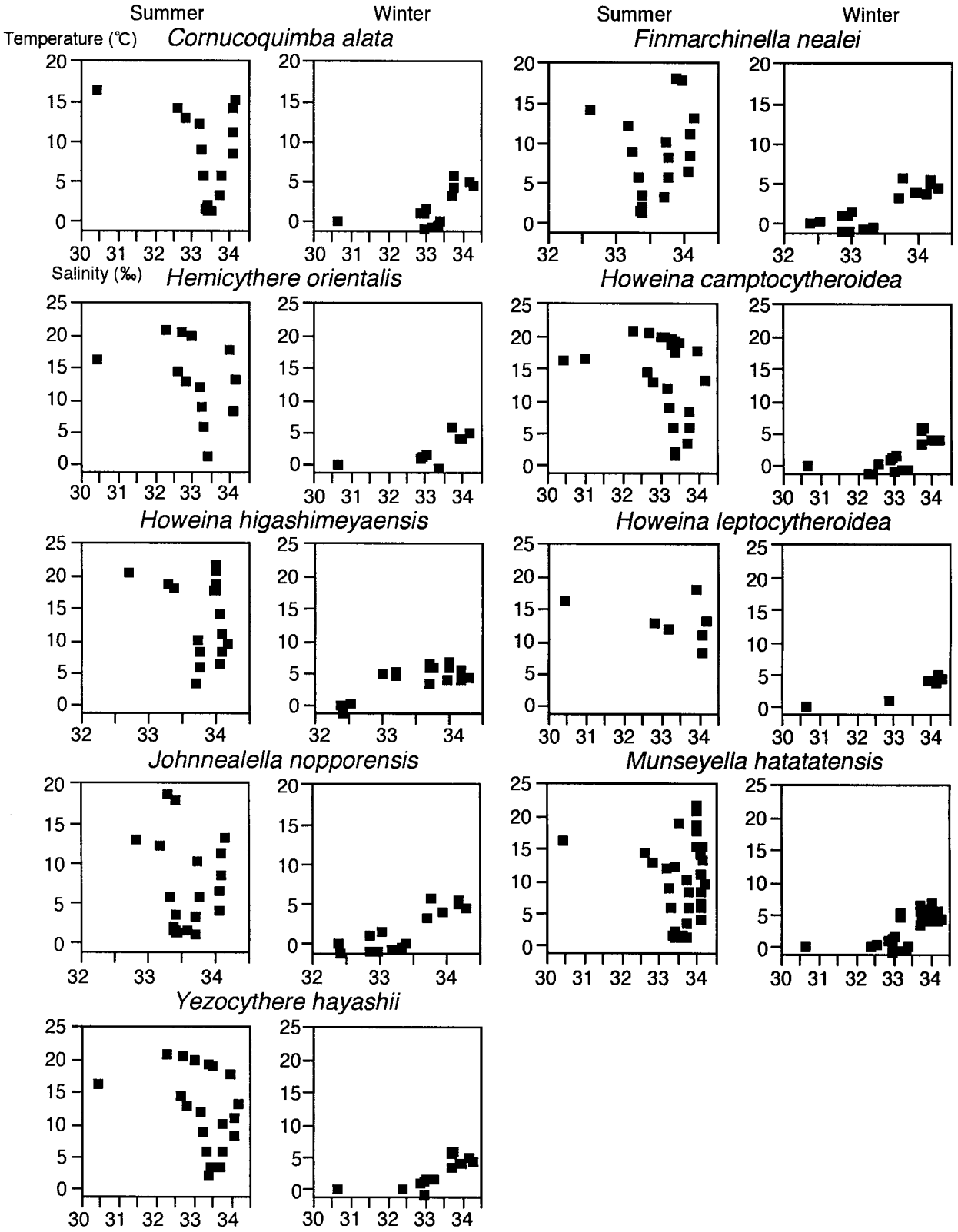


Figure 4. Temperature and salinity in summer (August, left graphs) and winter (February, right graphs) for nine species in the open sea-inner bay environment of Japan. A black square represents the temperature-salinity data at one water depth in one area.

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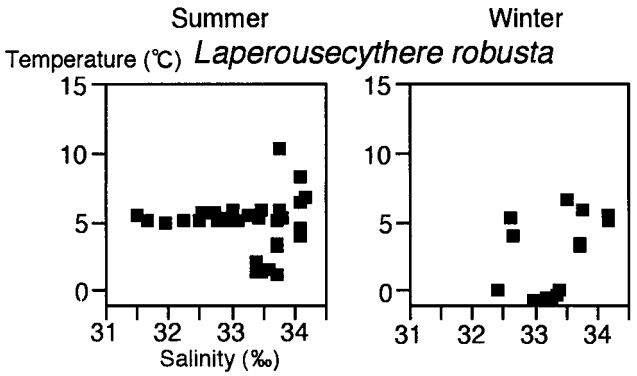


Figure 5. Temperature and salinity in summer (August, left graphs) and winter (February, right graphs) for the one species in the open sea environment of Japan-Alaska. A black square represents the temperature-salinity data at one water depth in one area.

distances quantitatively. Also in the case of the Japan Sea, Yellow Sea, northern Pacific and Otsuchi Bay, the distribution of the ostracod assemblages and the temperature-salinity characteristics of the water masses are clearly correlated (Brouwers, 1988; Zhao and Wang, 1988; Ikeya *et al.*, 1992; Zhou *et al.*, 1996; Ozawa, 1998, 2003a). Therefore, this study considers that the dead shells of ostracods examined here stay within the same water mass environments as the living condition on a scale of the inner bay and shelf – slope areas of the open sea, even if these shells are actually transported after their death to some degree.

Water temperature and salinity properties

The water temperature and salinity for the distributional areas in summer and winter were compiled for each species as shown in Figures 4–6. The

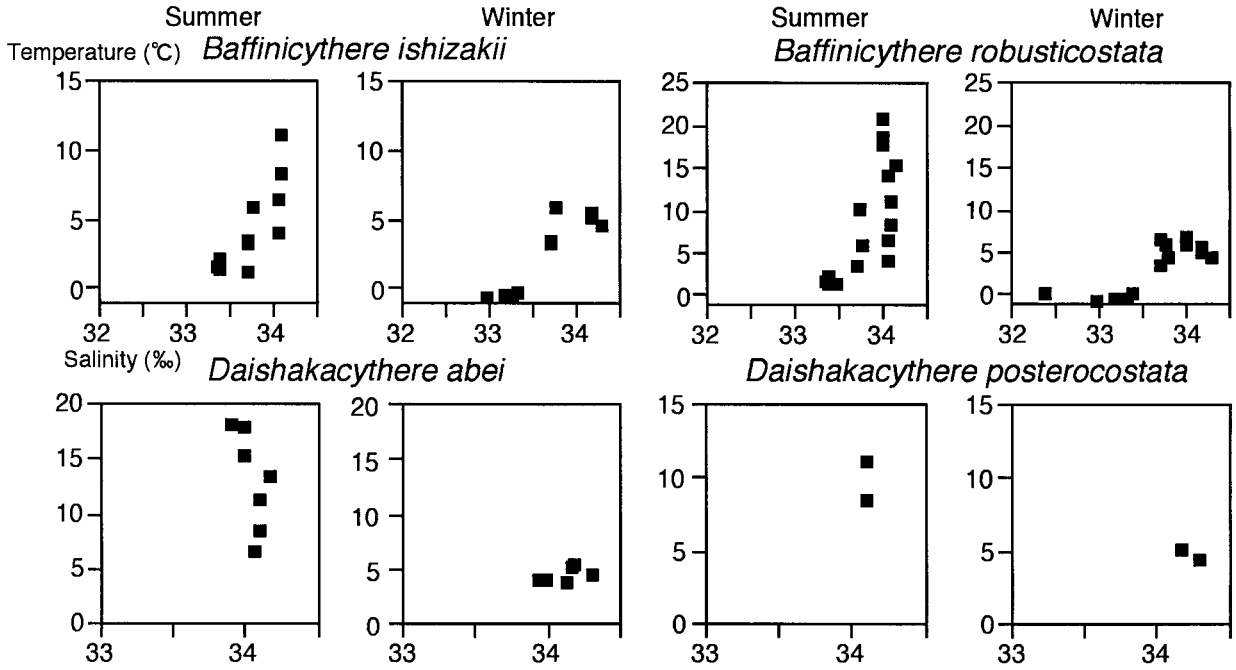


Figure 6. Temperature and salinity in summer (August, left graphs) and winter (February, right graphs) for the four species in the open-sea environment of Japan. A black square represents the temperature-salinity data at one water depth in one area.

Group name	Species number	Water depth (m)	Temperature (℃)		Salinity (‰)	
			Summer	Winter	Summer	Winter
Japan open sea-inner bay	9	1-250	0-20	0-5	30-34	30-34
Japan-Alaska open sea	1	15-493	around 5	0-5	31-34	32-34
Japan open sea	4	15-493	0-20	0-5	around 34	32-34

Figure 7. Summary of species numbers and marine environmental factors in the three groups for the fourteen species.

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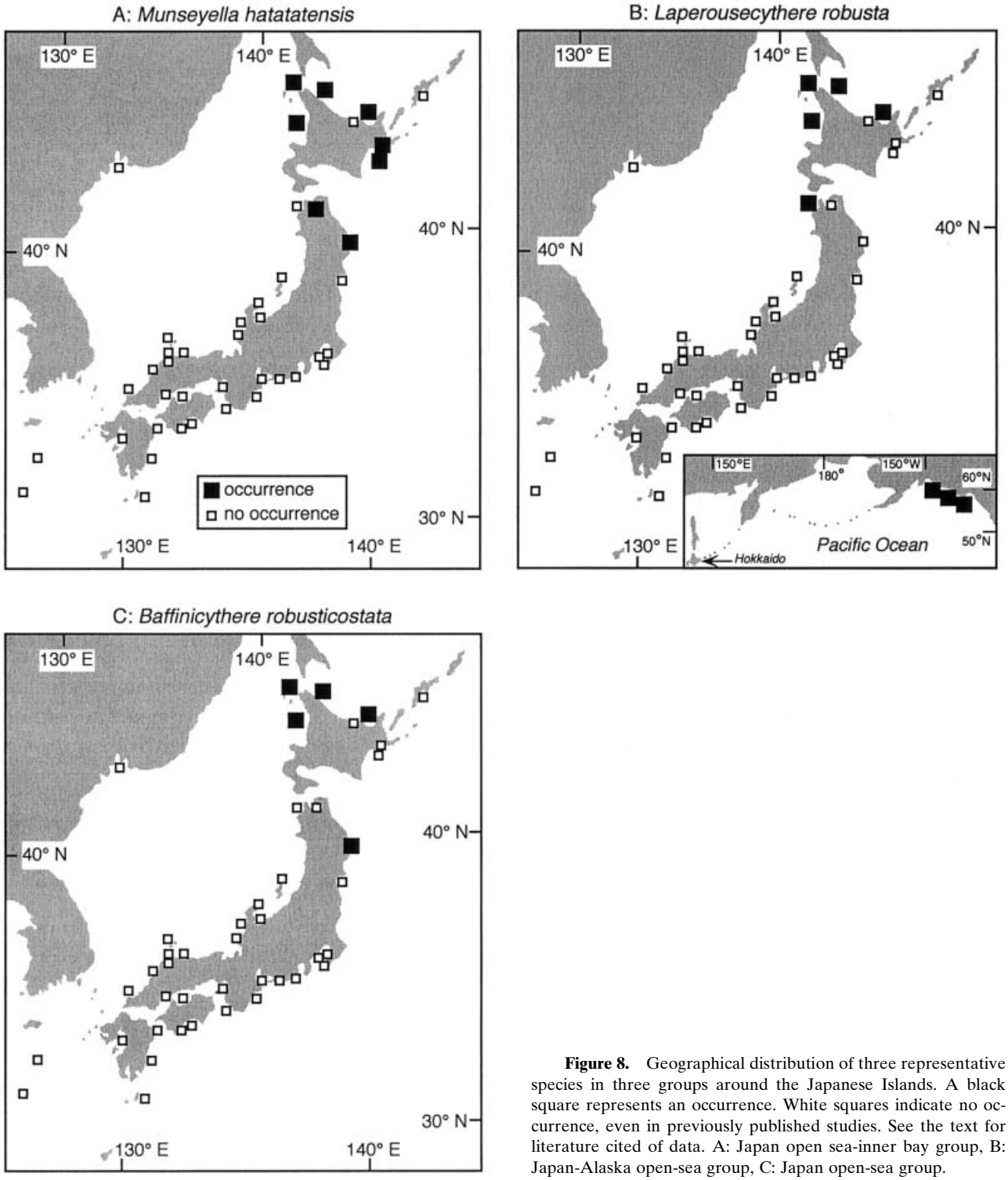


Figure 8. Geographical distribution of three representative species in three groups around the Japanese Islands. A black square represents an occurrence. White squares indicate no occurrence, even in previously published studies. See the text for literature cited of data. A: Japan open sea-inner bay group, B: Japan-Alaska open-sea group, C: Japan open-sea group.

temperature-salinity conditions in summer (left graphs in Figures 4–6), reflect the differences between the open sea-inner bay environments, and are divided into the following three species groups; (1) Japan open sea-inner bay, (2) Japan-Alaska open sea, (3) Japan open sea. The environmental conditions of the three groups are summarized in Figure 7. Figure 8 represents the Recent distribution of three species found from many

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areas of each group around the Japanese Islands. These occurrence data are cited from the same literature shown in the second chapter (Analytical methods).

In the Japan open sea-inner bay group, nine species are recorded: *Cornucoquimba alata*, *Finmarchinella nealei*, *Hemicythere orientalis*, *Howeina camptocytheroidea*, *H. higashimeyaensis*, *H. leptocytheroidea*, *Johnnealella nopporensis*, *Munseyella hatatatensis* and *Yezocythere hayashii*. This group shows the widest temperature range (0–20°C in summer; left graphs in Figures 4 and 7). This group also represents the widest salinity range (30–34‰). In winter, the distributional areas of these species shows temperatures less than 5°C, and salinity 30–34‰ (right graphs in Figures 4 and 7).

Only one species, *Laperousecythere robusta*, is distributed in the Japan-Alaska open sea-group. This environment is characterized in summer by the narrowest and the lowest range of the water temperature (around 5°C) and salinity (31–34‰) (left graphs in Figures 5 and 7). The winter condition is very similar to that in summer. This group shows the broadest geographical distribution, both in Japan and Alaska.

Baffinicythere ishizakii, *B. robusticostata*, *Daishakacythere abei* and *D. posterocostata* are distributed in the third environment, the Japan open-sea group. This environment is characterized by the widest temperature range, 0–20°C, with a maximum value of ca. 20°C (left graphs in Figures 6 and 7). Salinity shows the highest value and narrowest range at around 34‰. In winter, these species are distributed at temperatures less than 5°C and salinity 32–34‰ (right graphs in Figures 6 and 7).

The water temperature and salinity for all 14 species distributed in the three groups in summer and winter are shown together in Figure 9. According to the summer graph, there are two ranges of water temperature, a wide range of 0–20°C (left graphs A and C in Figure 9) and a narrow range around 5°C (left graph B in Figure 9). In contrast, in winter all of the species are distributed in conditions less than 5°C (right graphs A–C in Figure 9). On the salinity range, there are two ranges through the year; a wide range of 30–34‰ and a narrow range of 32–34‰. These data clarify that the so-called cold-water species inhabit wide-ranging temperature and salinity conditions.

Most of the ostracod species dealt with here, with the exception of the Japan-Alaska open-sea group *L. robusta*, are able to survive even at 20°C in summer, although they have been called cold-water species. All 14 species are distributed in the northern Japan Sea. Three other ostracod assemblages that lack these

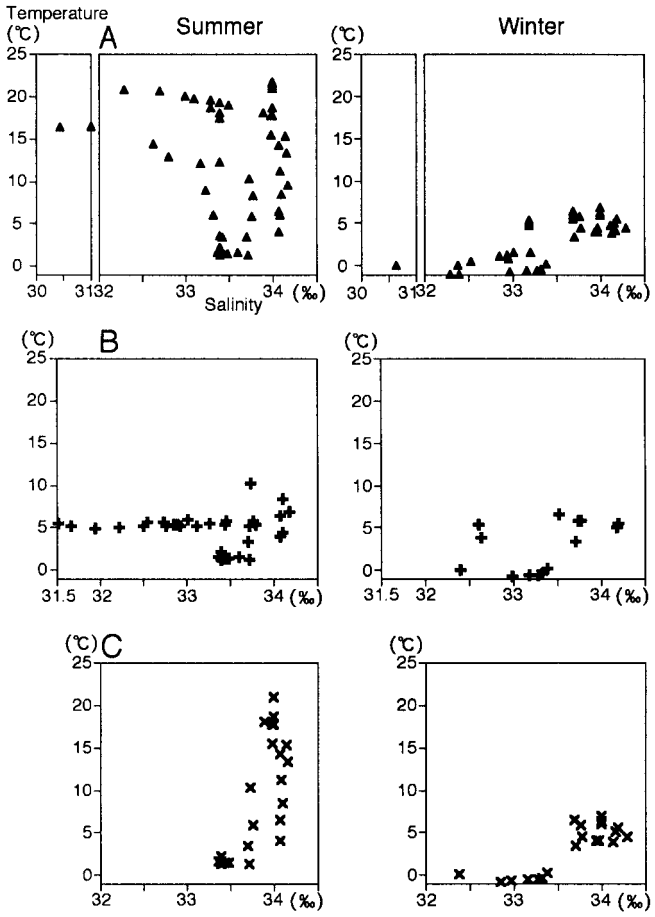


Figure 9. Summary of the water temperature and salinity in summer (August, left graphs) and winter (February, right graphs) for the distributional site of all the species in the three groups. One mark means the temperature-salinity data at one site of one water depth in one area. A: Japan open sea-inner bay group, B: Japan-Alaska open sea group, C: Japan open sea group.

14 cold-water species, also inhabit three major water mass environments in the Japan Sea – the Tsushima Warm Current Surface Water, the Tsushima Warm Current Core Water, and the Japan Sea Intermediate-Proper Water (Ozawa, 1998) (see the T-S range of graphs A–C in Figure 10). Comparing the temperature range for the 13 species in the two groups with the temperature of these major water masses in the Japan Sea, the range of 0–20°C of the two groups in this study includes those of all the three water masses, the Warm Current Surface Water, the Tsushima Warm Current Core Water, and the Japan Sea Intermediate-Proper Water (graphs A and C in Figure 10). In winter, all of the species are distributed in the low temperature condition of less than 5°C

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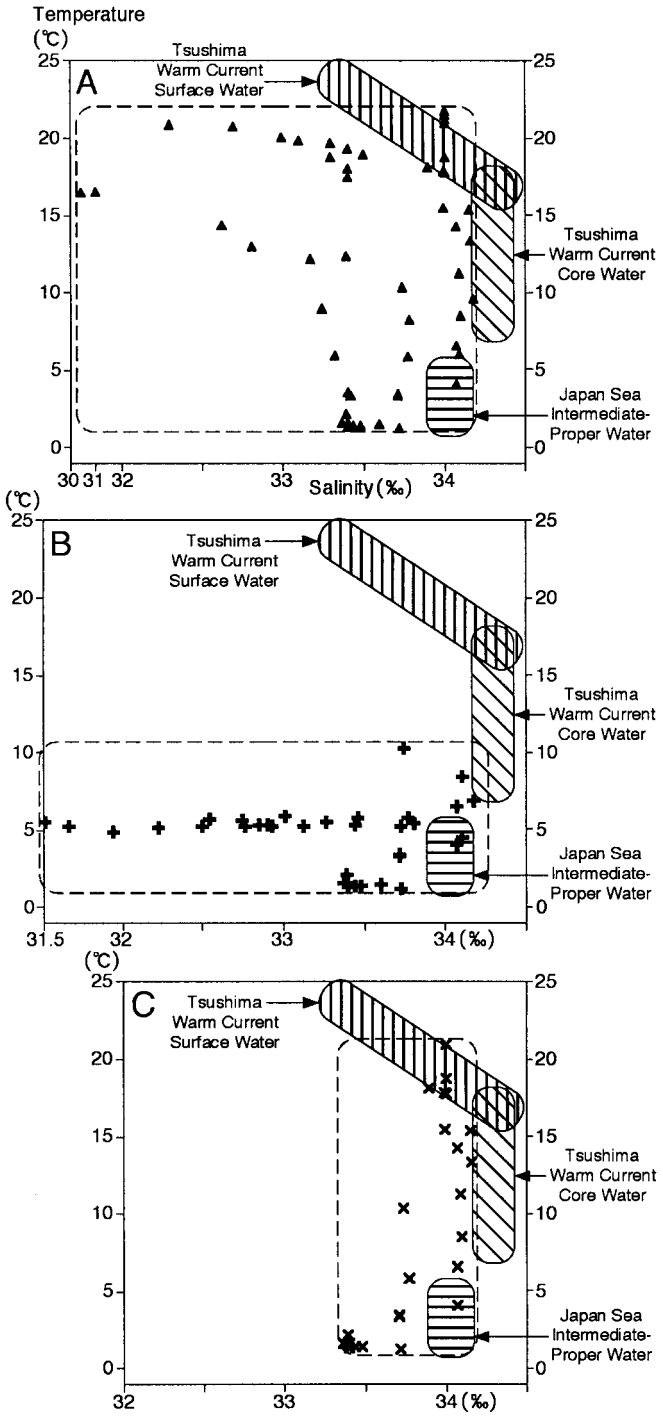


Figure 10. Temperature and salinity in summer (August) with the representative water masses for the three ostracod assemblages in the southern to northern Japan Sea of Ozawa (1998). One mark indicates the temperature-salinity data at one water depth in one area. A: Japan open sea-inner bay group, B: Japan-Alaska open-sea group, C: Japan open-sea group.

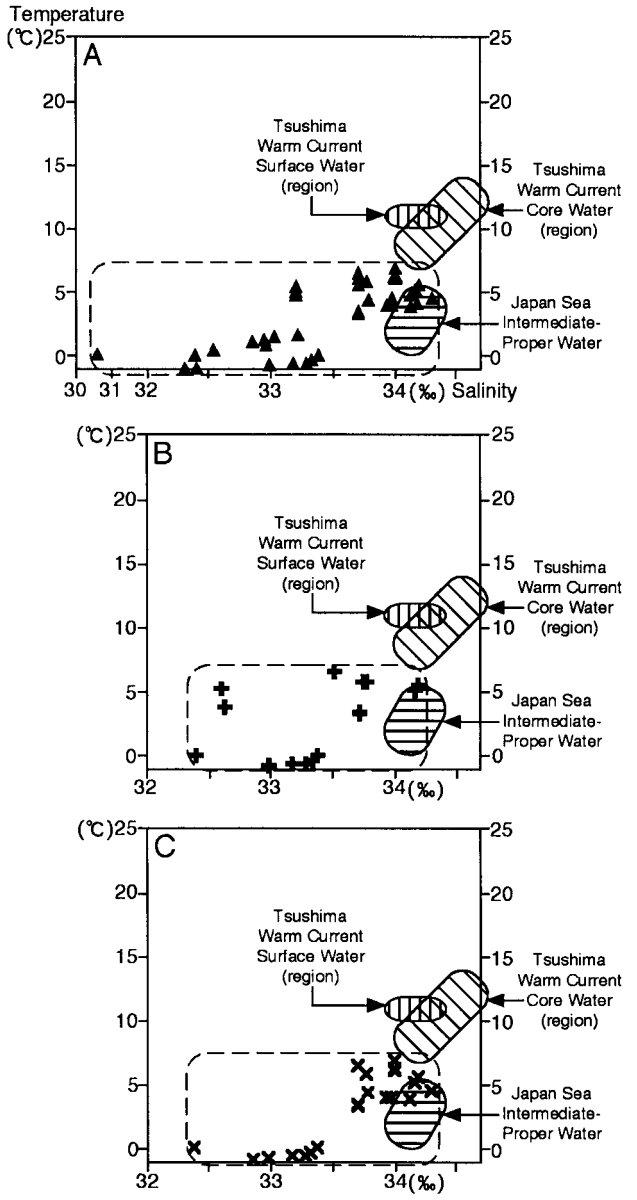


Figure 11. Temperature and salinity in winter (February) with the representative water masses for the three ostracod assemblages in the southern to northern Japan Sea of Ozawa (1998). One mark indicates temperature and salinity data at one water depth in one area. A: Japan open sea-inner bay group, B: Japan-Alaska open-sea group, C: Japan open-sea group.

(graphs A–C in Figure 11). This low water temperature is comparable to the Japan Sea Intermediate-Proper Water, the coldest water mass in this sea. Based on these results, 13 of the 14 species, *L. robusta* being the exception, have tolerance to relatively high temperature in summer up to 20°C.

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Discussion

Survival factors through the Pleistocene

Nine of the 14 species in the Japan open sea-inner bay group are distributed at the widest range of temperature and salinity, especially in summer (left graph A in Figure 9). Thus, it is considered that these species have a relatively high tolerance to temperature-salinity changes. However, their distributions are restricted by requiring winter water temperatures of less than 5°C (right graphs A–C in Figure 9). Based on the fossil record, most of these nine species had already appeared by the late Pliocene, around 3.0–2.0 Ma (e.g. Irizuki, 1989b). Thus, they have survived through the distinctive environmental fluctuations since the early Pleistocene, that is, the influx of warm-high salinity (warm current) water into the Japan Sea during each interglacial period. The influx of this water, which would be more than 7–10°C, even in winter, and salinities of 34–34.5‰ through the year (Figures 10 and 11), increased during interglacial periods when suitable temperature-salinity areas would become narrower than during glacial periods in and around the Japan Sea. However, these species can probably breed and maintain their populations even in small areas such as the restricted inner bay, when the large suitable areas of the open sea were repeatedly lost in the interglacial periods. The early Pleistocene Omma Formation in central Japan yields the maximum number of extinct ostracod species in the three families, more than 20 species from sediments of ca. 1.5 Ma, among the Pliocene and Pleistocene strata along the Japan Sea coast (Ozawa, 2001). These species are contained in the shallow-open sea fossil assemblages (Ozawa, 1996). Most species are not found in the open sea assemblages today, and have been considered to be extinct at least around Japan (e.g. Ozawa, 2001). Thus, the nine Recent species distributed in this environment are those which could survive during the interglacial and transitional periods, due to their various temperature-salinity tolerance in summer, not only in the open sea areas but also the inner bay regions.

Of these nine species, *Howeina camptocytheroidea* is also distributed in the northern Yellow Sea (Figure 12). The oldest fossil record of this species is reported from the late Pliocene Sasaoka Formation, northeastern Japan (2.20–2.05 Ma; e.g. Yamada *et al.*, 2002). This species also occurs from Pleistocene strata around the Yellow Sea (Zhao, pers. com.). Thus, *H. camptocytheroidea* migrated to the Yellow Sea from the Japan Sea, through the palaeo-Tsushima Strait in the Pleistocene. This species survived in the Yellow Sea during the Pleistocene environmental changes, probably due to relatively high tolerance to the wide T-S range in summer; it inhabits the northern area in winter conditions less than 5°C.

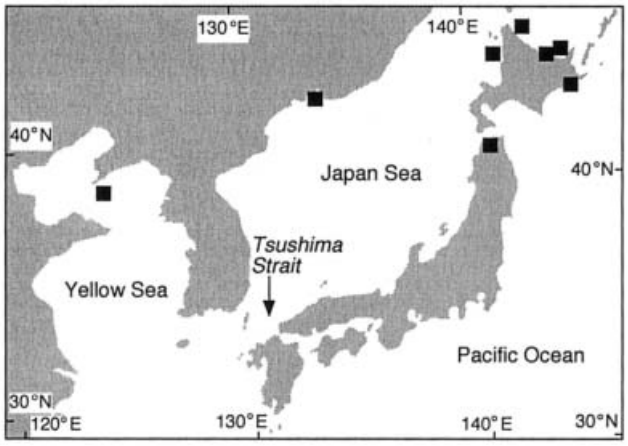


Figure 12. Recent geographical distribution of *Howeina camptocytheroidea.* Each black square represents an occurrence from one area.

Laperousecythere robusta in the Japan-Alaska open-sea environment has a very wide salinity tolerance (Figure 5, and graph B in Figure 9). This species is able to live in open-sea areas in relatively low salinity conditions, even as low as 31–32‰. *L. robusta* first appeared in the late Pliocene in the Japan Sea (e.g. Irizuki, 1989b). Later it occurred in the Alaska area during the Pleistocene (Brouwers, 1993). Based on its Recent temperature distribution, this species favors a temperature around 5°C through the year. According to the fossil record, this species migrated along the island arcs at the northwest and north Pacific regions, from the Japan Sea to the northeast Pacific after the late Pliocene, following its favored water temperature. This species inhabits the lower shelf region at ca. 150–200 m depths in the eastern Japan Sea, off Tsugaru (Figure 3), and dominates this environment where few other ostracod species exist (Ozawa, 1998; Tsukawaki *et al.*, 1999). No fossil occurrences of such an assemblage have been reported from any Pliocene and Pleistocene strata. It is considered that this species recently migrated to the deeper areas in the Japan Sea after the Pleistocene. *L. robusta* could survive, when the Pleistocene oceanic environment changed, through migration to the northern and deeper areas, where the temperature change must have been smaller than the shallow areas of the Japan Sea between glacial and interglacial periods.

In the third group of the open sea environment around Japan, four species are recorded, and they

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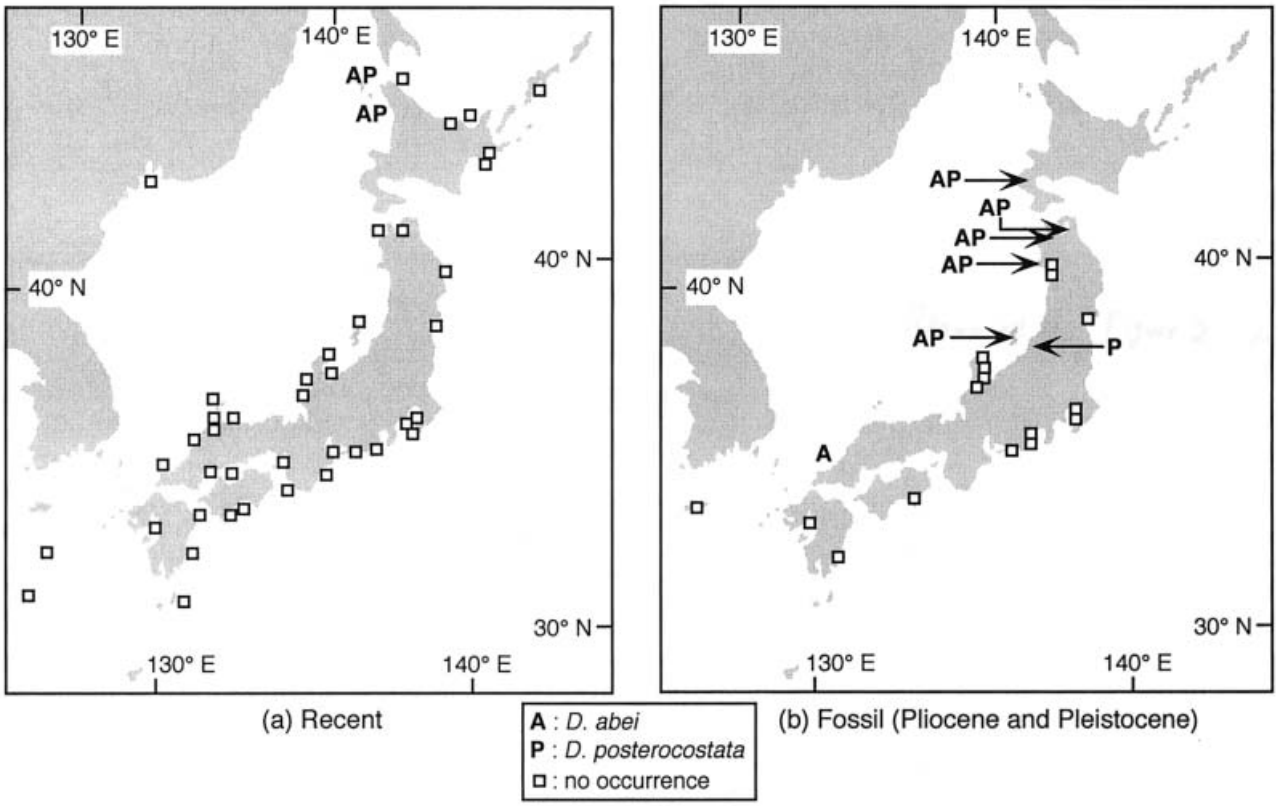


Figure 13. Geographical distribution of the two species of *Daishakacythere* in Recent and Pliocene-Pleistocene fossil records. See the text for literature cited.

survived during the Pleistocene. On the other hand, many species in the three families became extinct after 1.5 Ma in the Japan Sea (Ozawa, 2001). These four species flourished in the shallow-open sea during 1.2–0.4 Ma, replacing many extinct species in the same families. Thus the species composition of the open-sea ostracod assemblages changed considerably during this period (Ozawa, 2001). For example, the two species of *Daishakacythere* first appeared around 1.2 Ma, and flourished after 0.8 Ma at the latest in the Japan Sea (e.g. Tabuki, 1986). The distribution of *Baffinicythere robusticostata* expanded after 0.4 Ma in the Japan Sea (e.g. Irizuki, 1996a). The flux of warm water from the south during the interglacial periods became similar to the modern situation after 1.25 Ma (Kamiya *et al.*, 1996; Kitamura *et al.*, 2001; Ozawa and Kamiya, 2001). This event would produce an oceanic environment in this shallow sea, attaining temperatures of up to 20°C in summer and high salinity of 34‰ through the year. These species could invade and inhabit the newly appearing temperature-salinity conditions in the open sea after 1.25 Ma, and flourished there, replacing the extinct species. They have survived until today in the open sea along the Japan Sea.

The continuous presence of two *Daishakacythere* species only in the Japan Sea suggests that the modern salinity and oxygen levels of the northern Japan Sea existed during Pleistocene glacial periods. Suitable environmental conditions would have been maintained even during maximum glacial periods in the Japan Sea. The conditions are characterized by high salinity, around 34‰ (Figure 7) and high dissolved oxygen, 6–9 ml/l (e.g. Kuwahara, 1990). The fossil records of *Daishakacythere* characteristically exist from shallow-marine strata along the Japan Sea coast (e.g. Tabuki, 1986). In Figure 13, occurrences of *Daishakacythere* in Recent and fossil data are shown. Fossil records are cited from the literatures (Ishizaki, 1966, 1983; Ishizaki and Kato, 1976; Yajima, 1978, 1982, 1987; Ishizaki and Matoba, 1985; Ikeya *et al.*, 1985; Tabuki, 1986; Hanai and Yamaguchi, 1987; Paik and Lee, 1988; Nakao, 1993; Cronin *et al.*, 1994; Ozawa *et al.*, 1995; Irizuki, 1993, 1996b; Ozawa, 1996; Kamiya *et al.*, 1996, 2001; Tsukawaki *et al.*, 2000; Nakao *et al.*, 2001; Kamiya, unpublished data). Recent data were compiled from the same literature for Figure 8. The two *Daishakacythere* species first appeared around 1.2 Ma in northern Japan waters (e.g. Hanai and Yamaguchi,

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1987; Sugawara *et al.*, 1997). The youngest fossil record was reported from the southernmost area in the post-middle Pleistocene record (Ozawa, 2000; Tsukawaki *et al.,* 2000) (Figure 13).

Tada (1994) published a model of the water mass in the Japan Sea during glacial periods, which does not suggest suitable conditions for the survival of these species. His study is based on the planktic fossil faunas and floras from hemipelagic core sediments of ca. 3,000 m water depths in the central sea. His model consists of two water layers: a low salinity water cap with fresh water input at the surface and anoxic deeper water. If his model is correct, these two *Daishakacythere* species could not inhabit either water mass, because they require both high salinity and oxygen conditions similar to the present. However, these two species have survived since the Pleistocene only in the Japan Sea (Figure 13). Therefore, it is possible that high salinity, around 34‰ but not an anoxic environment, was maintained in the shallow area in a part of the Japan Sea in the glacial period.

This estimation is supported by studies on other Japan Sea faunas after the Pliocene, from which the existence of the high salinity and oxygenated water masses during the glacial periods since the middle Pleistocene and the Last Glacial period (18–15 ka) is inferred. One example is a study of the benthic gastropods Buccinidae and Ancistrolepidinae, with eight molluscan species in other families (Amano and Watanabe, 2001). Their study estimated that living water depths during glacial periods since the middle Pleistocene was ca. 100–400 m. Another example is the planktic radiolarian *Ceratospyris borealis* (Itaki *et al.*, 1996; Itaki, 2001). These radiolarian studies inferred that the required depth of *C. borealis* in the Last Glacial Period was ca. 200–300 m or shallower than 160 m. Two Recent *Daishakacythere* ostracod species are found from ca. 20–100 m in the northern Japan Sea (Figure 3). Thus, it is highly probable that these ostracods have survived in the bottom water on the shelf, and that a suitable high salinity and oxygen water mass existed along the coast even during the glacial period.

Based on these considerations, the fourteen Recent ostracod species in the three environments have survived in or around the Japan Sea through the Pleistocene, due to their wide temperature-salinity tolerance. The cold-water ostracods may be divided into those which survived and those which became extinct during the Pleistocene. The 14 species dealt with here belong to the former group. They have survived cyclic environmental changes, linked with the glacio-eustatic sea-level changes since the early Pleistocene, until today in and around the Japan Sea. Species of the families Hemicytheridae and Cytheruridae, characteristically in open-sea fossil assemblages with no modern occurrences (e.g. Ozawa, 2001; Ozawa and Kamiya, 2001), could not survive the repeated environmental changes during the Pleistocene. They probably became extinct due to relatively low tolerance to the large T-S fluctuations.

Cold-water environment in the palaeo-Japan Sea

Previous studies of water conditions in the shallow sea where high-diversity benthic faunas flourished during glacial periods in the Pliocene and Pleistocene Japan Sea have given us a broad view of the cold or cool-water conditions. An example of the palaeotemperature in the shallow-cold water area in the early Pleistocene is given by Amano (1993), who estimated the specific range based on the species compositions of the molluscan *Mizuhopecten-Glycymeris* assemblage from 10 strata along the coast. Amano showed only the annual surface water temperature, and stated that these estimated values have several problems. Cronin *et al.* (1994) estimated the palaeobenthic temperature in summer and winter in the shallow sea (estimated 20–40 m depth) for glacial periods in the late Pliocene 2.7–2.3 Ma. They investigated the fossil ostracods, including many cold-water species in the three families from the Yabuta Formation, central Japan, using the Modern Analog Technique method (MAT) of dissimilarity coefficients to compare Recent and fossil assemblages around Japan. Their estimated palaeo-temperature is ca. 15–17°C in summer and 4–7°C in winter for the eight glacial periods. However, these estimates were based on Recent data containing very few cold-water ostracods in three families, so their temperature estimates have some problems. Data on the Recent distribution of cold-water ostracods around Japan has increased since the latter half of the 1990's. These ostracods inhabit a relatively wide range of summer temperature (0–20°C) and low winter temperature range (less than 5°C) (Figure 9). Therefore we consider Cronin *et al.*'s winter temperature range of 4–7°C to be slightly high, and their summer temperature range of 15–17°C to be too high.

Most of these 14 species belong to genera such as *Baffinicythere*, *Finmarchinella* and *Hemicythere*, which inhabit higher latitudes than the Japan Sea today (e.g. Tabuki, 1986). These ostracods often occur together as fossils with the Omma-Manganji molluscan fauna, generally cold-water or cold-current species, from the Pliocene and Pleistocene strata (e.g. Cronin and Ikeya, 1987). Based on the temperature ranges deter-

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mined in this study, the greatest difference with the warm Tsushima Current Water region, e.g., on the continental shelf at the southern to eastern Japan Sea, is the winter temperature (Figure 11). The Pliocene and Pleistocene fossil assemblages containing summer temperatures of these 14 species are inferred to have winter temperatures of 0–5°C, and 0–5°C or less than 20°C in summer. The low temperature, especially in winter, has obstructed colonization by species which favor warm-current water, defined as greater than 7–10°C, even in winter (Figure 11). Thus, the appearance of the fossil assemblages containing abundant cold-water ostracods with few warm-water species suggests intense cold-water conditions for many years.

Winter temperatures of 0–5°C are probably important for survival of these 14 species. The water depth difference is not as significant, since the distribution of such species in the Japan-Alaska open sea group was reported from a wide depth range ca. 20–500 m (Figure 7).

A winter temperature of less than 5°C and salinity less than 34‰ through the year for the 14 cold-water species in the three families in the Omma-Manganji ostracod fauna are the key factors for the interpretation of shallow-sea environments during glacial periods in the Pliocene and Pleistocene Japan Sea.

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