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Biogeography and the Pleistocene extinction of neogastropods in the Japan Sea

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Abstract

During the middle to late Pleistocene glacial lowstands, when the Japan Sea was almost isolated geographically, low-salinity surface water and anoxic deep water were formed. Pliocene to early Pleistocene buccinid gastropods which mainly lived deeper than the lower sublittoral zone underwent extinction owing to anoxic deep water. On the other hand, upper–sublittoral muricid and buccinid species suffered from extinction due to decrease of surface salinity. However, fossil records indicate that species in the Pacific Ocean east of Japan having shallow minimum depths reinvaded the Japan Sea through shallow, northern straits at least in the latest Pleistocene. The fossil and Recent records of two *Buccinum* species restricted to the Japan Sea side indicate normal salinity and oxic water at ca. 100–400 m during glacial lowstands.

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1. Introduction

The Japan Sea is a marginal sea located within a semi-enclosed basin that is connected to the open ocean through shallow straits: Tsushima Strait (130 m in depth), Tsugaru Strait (130 m), Soya Strait (55 m) and Mamiya Strait (15 m) (Fig. 1). Based on the presence of black layers in deep-sea cores, the deeper-water portions of the Japan Sea became euxinic in the glacial Pleistocene (Tada, 1994). The surface water became brackish in the Ice Ages, owing to the input of fresh water (Oba et al., 1991), and such a strong

environmental change altered the distribution of the benthic fauna. Matoba (1978, 1984) has pointed out that almost all the deep-water benthos underwent extinction in this late Pleistocene euxinic environment, and Valentine and Jablonski (1991) have suggested that Quaternary eustatic sea-level change should have influenced the extinction of endemic populations in marginal seas. However, little is known about the relationship between the hydrographic stratification of a marginal sea during glaciation and the extinction of benthic fauna.

Among neogastropods, most temperate and boreal species of buccinids and muricids are known to be predators, and have non-planktotrophic larvae, which are not an effective mode of distribution (Strathmann, 1987). Owing to the difficulties

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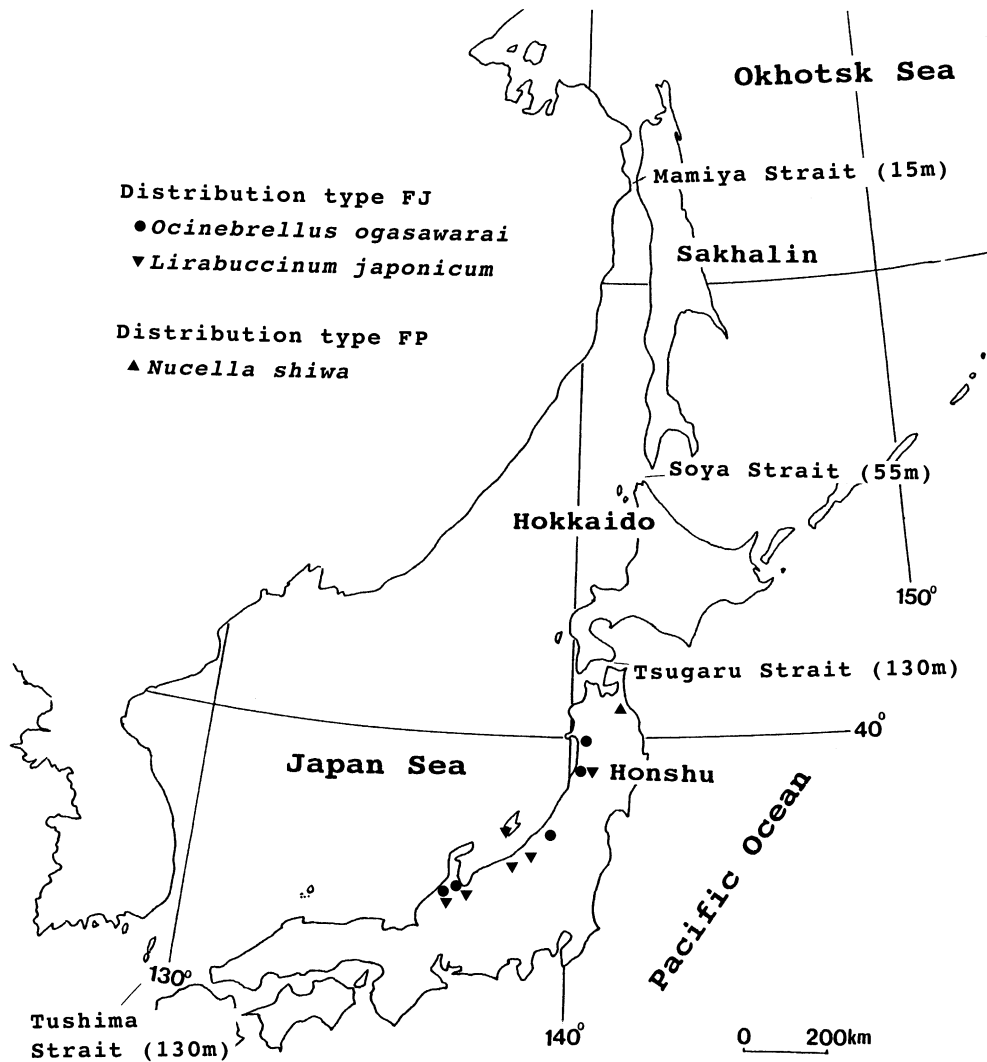


Fig. 1. Distribution of extinct species *Ocinebrellus ogasawarai*, *Lirabuccinum japonicum* and *Nucella shiwa*. The first two species occurred from the Pliocene and lower Pleistocene only in the Japan Sea borderland (distribution type FJ), the last from the Pliocene only in the Pacific side (distribution type FP). Also shown are the depths of straits of the Japan Sea.

of dispersal, deep-water non-planktotrophic gastropod groups with restricted distribution seem especially vulnerable to extinction resulting from environmental change. Bouchet and Warén (1979) and Bouchet and Taviani (1992) showed that distribution of most deep-water gastropods with non-plankton stage are restricted in each deep-sea basins. In fact, the biogeography of some deep-water buccinids reflects extinction caused by euxinic bottom conditions in the enclosed Japan Sea

during the Pleistocene Ice Ages (Amano et al., 1996; Amano, 1997; Amano and Watanabe, 2001).

On the other hand, many boreal shallow-water gastropods with non-planktonic larval stage achieve very broad ranges perhaps by floating and rafting on seaweed or wood (Vermeij et al., 1990; Reid, 1996). It may be possible for them to cross the shallow seaways and to expand their distribution broadly. Thus, they seem to have tol-

erated the deteriorating environment in the glacial age. However, the distribution of shallow-water neogastropods has not yet been examined in detail.

In this study, I examine the biogeography of shallow-water neogastropods, comparing it with that of deep-water ones. I also reconstruct the paleoceanographic conditions of the Japan Sea during the glacial age from the biogeographical point of view.

2. Materials and methods

For reconstructing the hydrographic stratification of the Japan Sea, I examine the distributional types of the deep-water (DW) and shallow-water taxa (SW) separately. The DW group comprises the boreal buccinids Ancistrolepidinae, *Neptunea* and *Buccinum*, mainly living in lower-sublittoral to bathyal depths in the northwestern Pacific (Higo et al., 1999). Their distribution types in the Pliocene and early Pleistocene are relatively well known (Amano et al., 1996; Amano, 1997; Amano and Watanabe, 2001). The SW group comprises the boreal, shallow-water muricids *Nuccella*, *Ceratostoma*, and the buccinid *Lirabuccinum*, as well as the temperate, shallow-water muricid *Ocenebrellus*. They are rocky-bottom dwellers in intertidal to upper-sublittoral depths. *Ceratostoma*, *Ocenebrellus* and *Lirabuccinum* have previously been taxonomically examined in detail (Amano and Vermeij, 1998a,b, 2003).

Distribution of these Pliocene and early Pleistocene taxa can be subdivided according to several types as Amano (1997) and Amano and Watanabe (2001) did. The type is based on combinations of fossil and Recent occurrences. They seem to reflect origination in the Pliocene to early Pleistocene and extinction and migration in the marginal sea during the middle to late Pleistocene. Fossils occur in Pliocene and early Pleistocene faunas on only the Japan Sea side, only on the Pacific side, or on both sides of Japan. Extant Pliocene and early Pleistocene species now live in the Japan Sea, in the Pacific Ocean, or in both areas. In this paper, the Japan Sea borderland includes areas along the Tsugaru Strait and

southwestern Hokkaido, because the Pliocene to early Pleistocene endemic fauna of the Japan Sea, the Omma–Manganji fauna (Otuka, 1939) also occurs in these areas.

Fossil and Recent specimens examined in this paper are housed at the following institutions and museums: the Joetsu University of Education (JUE), Tohoku University Museum (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), University of Tsukuba (IGUT), University Museum of University of Tokyo (UMUT), National Science Museum (NSM), and Kyoto University (JC).

3. Types of distributional patterns

Twelve types of distribution patterns are theoretically possible, but only eight (listed in Tables 1 and 2) are recognized among the taxa mentioned above, with the DW group having a higher diversity of species and distribution types than the SW group.

A total of six distribution types (FJ, A, B, C, D, and E), comprising 36 species, are recognized in the DW group (Amano and Watanabe, 2001). Type FJ (11 species) comprises extinct species which are endemic to the Japan Sea borderland (Table 1). Type A (9 species) consists of species which suffered extinction in the Japan Sea, but are still living in the North Pacific, Okhotsk and Bering Seas. Types FJ and A dominate the DW group (20 species, or 56% of total species). Type E species (2 species) live and occur as fossils only in the Japan Sea. Type B species (5 species) occur as fossils along the Japan Sea margin, but now live in the northern Japan Sea, as well as the Northwest Pacific and Okhotsk Sea. They might have originated in the Japan Sea. Type C species (3 species) are known as fossils from the Pacific and the Japan Sea coasts and still live in both regions. Type D species (6 species) live only on the Pacific side, and have been recorded as fossils only from there.

Five distribution types (FJ, B, C, C', FP) comprising 10 species are recognized in the SW group. Among them, types C' and FP are first recognized here. The type C' species, *Ceratostoma fournieri*,

Table 1
Distribution types of the DW group (after Amano and Watanabe, 2001)

Distribution types	Fossil	Recent	<i>Buccinum</i>	<i>Neptunea</i>	Ancistrolepidinae
FJ	Japan Sea side	(Extinct)	<i>B. sinanoense</i> , <i>B. shibatense</i> , <i>B. saitoi</i>	<i>N. eos</i> , <i>N. hataii</i> , <i>N. nikkoensis</i>	<i>Ancistrolepis masudaensis</i> , <i>A. koyamai</i> , <i>A. peulepis</i> , <i>A. aff. hikidai</i> , <i>Clinopegma fragilis</i>
A	Japan Sea side	North Pacific, Okhotsk Sea, Bering Sea	<i>B. rhodium</i> , <i>B. unscarinatum</i>	<i>N. lamellosa</i> , <i>N. satura</i> , <i>N. insularis</i> , <i>N. vinosa</i>	<i>Ancistrolepis grammatus</i> , <i>Clinopegma borealis</i> , <i>Bathyancistrolepis trochoideus</i>
E	Japan Sea side	Japan Sea	<i>B. striatissimum</i> , <i>B. tsubai</i>	–	–
B	Japan Sea side	North Pacific, Okhotsk Sea, Bering Sea/ N. Japan Sea	<i>B. middendorffi</i> , <i>B. inclytum</i>	<i>N. lyrata</i> , <i>N. bulbacea</i> , <i>N. rugosa</i>	–
C	Pacific/ Japan Sea sides	Pacific/Japan Sea	<i>B. ochotense</i>	<i>N. intersculpta</i> , <i>N. arthritica</i>	–
D	Pacific side	Pacific	<i>B. leucostoma</i> , <i>B. bulimiloideum</i>	<i>N. kuroshio</i> , <i>N. fukuaeae</i> , <i>N. kanagawaensis</i>	<i>Clinopegma unicum</i>

Types FJ and A, which underwent extinction in the Japan Sea, dominate the DW group (56% of total species).

is known as a fossil only along the Pacific coast, but now lives in both the Japan Sea and the Pacific (Fig. 2; Table 2). The type FP species, *Nucella shiwa* is extinct and confined to the Pacific side (Fig. 1). The other types of the SW group, FJ, B and C, show the same combinations as their counterparts in the DW group. *Ocinebrellus ogasawarai* and *Lirabuccinum japonicum* are extinct species whose distributions are confined to the Japan Sea borderland (Type FJ; Fig. 1). *Ocinebrellus lumarius* is in type B (Fig. 3), while *Nucella freycineti*, *Ocinebrellus inornatus*, *O. aduncus* and *Lirabuccinum fuscolabiatum* are in type C (Fig. 2).

Ceratostoma brunetti has been recorded only from the lower Pleistocene Tomikawa Formation along Tsugaru Strait (Amano and Vermeij, 1998b). As mentioned above, the Japan Sea borderland includes areas along the Tsugaru Strait and southwestern Hokkaido. *Ceratostoma brunetti* can be treated as the species in type B. The type B species might originate in the Japan Sea or the Tsugaru Strait area. In contrast with the DW group, all Recent species of the SW group belong to types B, C and C'. No species of types A, E and D are present in the SW group.

In addition to these characteristics, within the

Table 2
Distribution types of the SW group

Distribution types	Fossil	Recent	<i>Nucella</i>	<i>Ceratostoma</i>	<i>Ocinebrellus</i>	<i>Lirabuccinum</i>
FJ	Japan Sea side	(Extinct)	–	–	<i>O. ogasawarai</i>	<i>L. japonicum</i>
B	Japan Sea side (Tsugaru Strait area)	N. Pacific–Bering Sea/ Japan Sea	–	<i>C. brunetti</i>	<i>O. lumarius</i>	–
C	Pacific/Japan Sea sides	Pacific/Japan Sea	<i>N. freycineti</i>	–	<i>O. inornatus</i> , <i>O. aduncus</i>	<i>L. fuscolabiatum</i>
C'	Pacific side	Pacific/Japan Sea	–	<i>C. fournieri</i>	–	–
FP	Pacific side	(Extinct)	<i>N. shiwa</i>	–	–	–

All Recent species belong to types B, C and C'. No species of types A, E and D are present in the group.

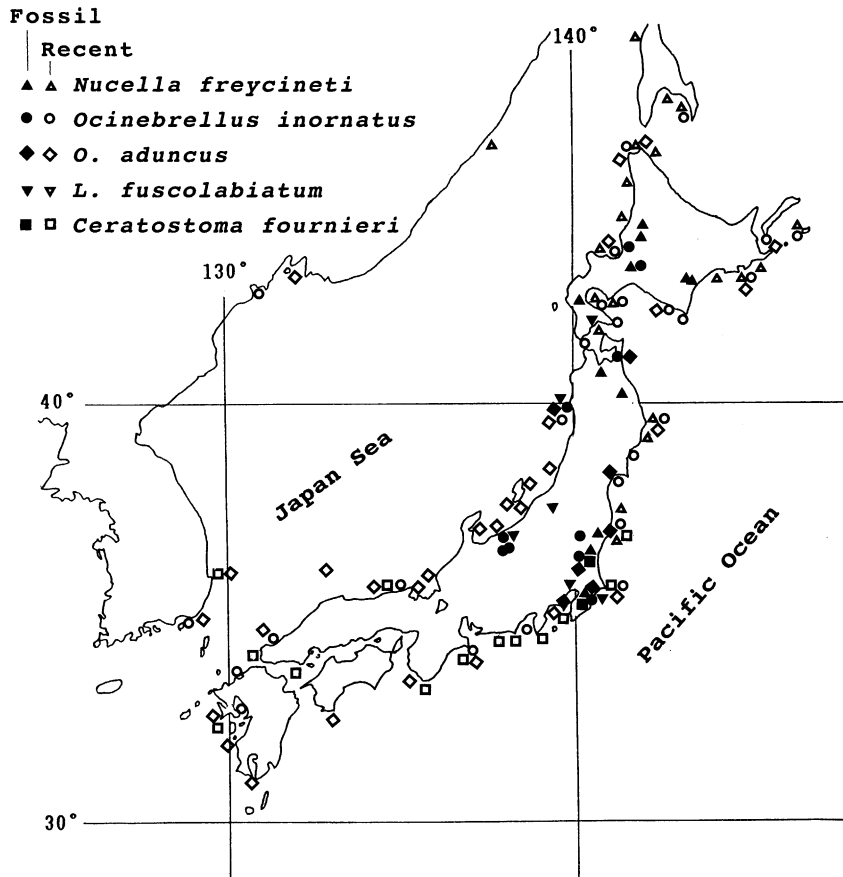


Fig. 2. Distribution of extant species *Nucella freycineti*, *Ocinebrellus inornatus*, *O. aduncus*, *Lirabuccinum fuscolabiatum*, and *Ceratostoma fournieri*. All of them are now living both in the Japan Sea and Pacific Ocean sides. Fossils of the first four species have been recorded also from both seas (distribution type C) while the last one has fossil records only on the Pacific side (distribution type C'). They did not suffer from extinction by the deteriorated environment during the glacial lowstands because there are populations also on the Pacific side.

DW group, species of types A, E and D are restricted to the Japan Sea or the Pacific, and these species now dwell only in water deeper than 50 m (Fig. 4). In contrast, the minimum depths of species in types B and C of the DW group are shallower than 50 m. In comparison, all Recent species in the SW group belong to types B, C and C', and all of them can live intertidally now.

4. Discussion

Based on oxygen isotope ratios, color of sediments, geochemical data of deep-sea sequences,

Tada (1994) inferred that low-salinity surface water and anoxic deep water formed during Pleistocene glacial lowstands, when the Japan Sea was almost isolated geographically.

Based on oxygen isotope data, surface-water salinity in the Japan Sea might have decreased to 24–28‰ at the Last Glacial Maximum (Tada, 1995; Oba, 1995; Gorbarenko and Southon, 2000). These data and Tada's model imply that, during any given Pleistocene glacial stage, salinity might have decreased. Most muricid species are stenohaline, living at 28–34‰ salinity (Egorov, 1993). Thus, decreased surface salinity likely caused extinction of the two shallow-water

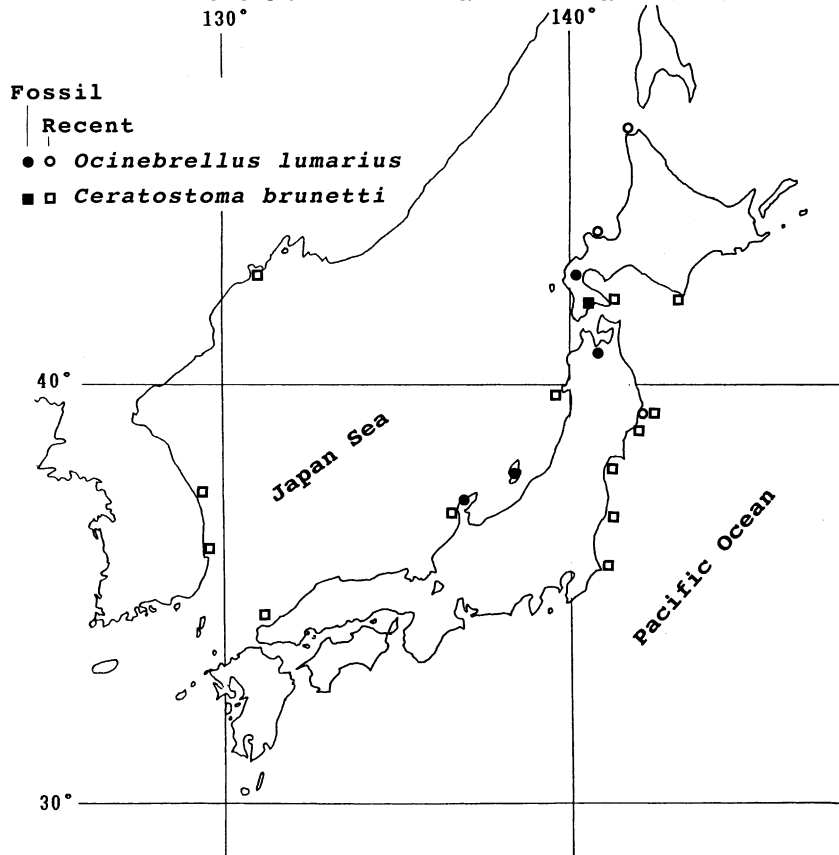


Fig. 3. Distribution of extant species *Ocinebrellus lumarius* and *Ceratostoma brunetti*. Like distribution types C and C', they are now living both in the Japan Sea and the Pacific, but their fossil records are restricted to the Japan Sea borderland (distribution type B). They might originate in the Japan Sea or the Tsugaru Strait area and then have expanded their distribution to the Pacific side.

Pliocene to early Pleistocene Japan Sea species (the type FJ species of the SW group; Fig. 5). However, it is difficult to identify the glacial lowstands which caused such extinction.

In contrast, as noted above, populations of types A and FJ in the DW group underwent extinction in the Japan Sea probably owing to anoxic conditions during any glacial lowstands in the middle to late Pleistocene. The populations of the North Pacific, Okhotsk and Bering Seas type A species survived during the Ice Ages (Amano et al., 1996).

Thus, most shallow- and deep-water species, including types B and C, once suffered from extinction (Amano, 1997). Such extinction is recognized in the benthic foraminifera during the late

Pleistocene (Matoba, 1978; Oba, 1995). On the other hand, the type E species survived in the lower-sublittoral to upper-bathyal waters (ca. 100–400 m) of the Japan Sea, which were presumably of normal salinity and oxic during the glacial lowstands (Amano and Watanabe, 2001). The existence of fully marine water is supported by Itaki et al. (1996) and Itaki (2001), who inferred normally saline and oxic water at depths of 200–300 m in the Japan Sea during the Last Glacial episode (18–15 kyr BP), based on the occurrence of radiolarian fossils from deep-sea cores of the eastern Japan Sea.

In the Mediterranean Sea, the shallow depths of straits prevent colonization by non-planktonic, deep-water dwellers (Bouchet and Taviani,

1992). According to Kitamura et al. (2001), this northern strait became narrow and/or shallow even during interglacial highstands in the Pleistocene. After the extinction of shallow- and deep-water dwellers in the Japan Sea during the Ice Ages, the type FJ, A and D species could not cross the shallow northern strait between the Japan Sea and the Pacific because they lived only in water deeper than 50 m (Fig. 5). On the other hand, the surviving population of types B, C and C' species of both SW and DW groups on the Pacific side could reinvade the Japan Sea because of their shallow minimum depths. At least in the latest Pleistocene (15–10 kyr), the cold-water Oyashio Current flowed into the Japan Sea via the Tsugaru Strait (Oba, 1995) and reintroduced a shallow, boreal fauna into it.

According to Valentine and Jablonski (1991), the extinction rate of neritic invertebrates during the Ice Ages was remarkably low. However, the extinction of benthic fauna in a marginal sea was affected by environmental change during glacial lowstands, while anoxic events caused extinction during a warming climate with a marine transgression (Hallam and Wignall, 1997). In contrast, in marginal seas both euxinic and anoxic events occurred during the cold climate age.

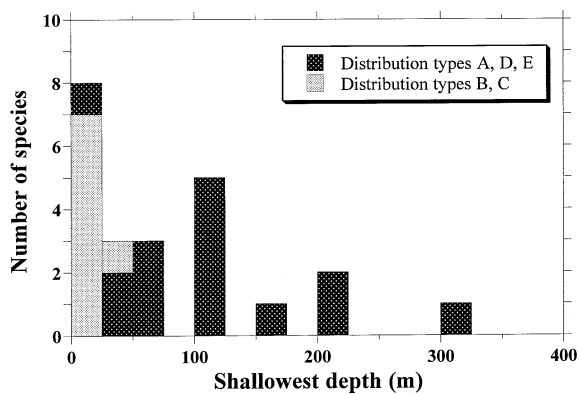


Fig. 4. Frequencies of shallowest depths of Recent species in the DW group. Except for three species, type A, D and E species do not live shallower than 50 m, other than three species. On the other hand, all type B and C species, living both in the Japan Sea and the Pacific, can also dwell shallower than 50 m.

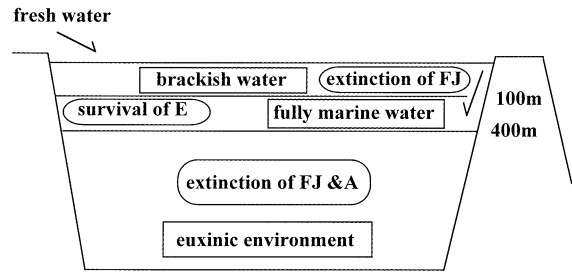


Fig. 5. Interpretation of paleoceanographic stratification and response of benthic fauna during middle to late Pleistocene glacial lowstands. Type FJ species underwent extinction because of the decreased saline surface water while the types FJ and A species did because of the euxinic bottom water. Type E species survived in fully marine water at ca. 100–400 m depth.

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