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SHORT COMMUNICATION

First report of *Osedax* in the Indian Ocean indicative of trans-oceanic dispersal through the Southern Ocean

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Abstract

Three specimens of the bone-eating worms, *Osedax rubiplumus* Rouse, Goffredi & Vrijenhoek, 2004, were collected from pig bones deployed in the periphery of Longqi vent field on the Southwest Indian Ridge (SWIR). *Osedax rubiplumus* was previously only reported in both the eastern and western North Pacific and Antarctic oceans. Our finding extends its range to the Indian Ocean, representing a much wider distribution of *O. rubiplumus* than previously expected. Moreover, all individuals of *O. rubiplumus* from the SWIR form a single haplotype with the highest divergence from the Pacific ones.

Keywords *Osedax rubiplumus* · New record · Biogeography · Southwest Indian Ocean

Introduction

The *Osedax* spp., commonly known as bone-eating worms, are exclusively associated with vertebrate carcasses (Rouse et al. 2018). They are well known for their life histories (e.g., such as dwarf males and propagation), specialized adaptations to bone remains, and associations with heterotrophic bacteria endosymbionts (Katz et al. 2011; Rouse et al. 2004, 2015; Tresguerres et al. 2013). To date, a total of 26 described species and 9 currently undescribed but putatively new species have been reported from oceans almost all around the world, except for the Indian Ocean (Fujiwara et al. 2019; Rouse et al. 2018; Salathé and Vrijenhoek 2012; Shimabukuro and Sumida 2019; Taboada et al. 2015). Of them, 19 species (including 1 operational taxonomic unit (OTU)) were reported from Monterey Bay in the eastern North Pacific—revealing a remarkable diversity there (Rouse et al. 2018; Vrijenhoek et al. 2009), 9 (including 3 OTU) from the western North Pacific (Fujikura et al. 2006; Fujiwara et al. 2019), 6 from the Southern Ocean (Amon et al. 2014; Li et al. 2017; Glover et al. 2013), 6 (including 4 OTU) from the South Atlantic (Fujiwara et al. 2019; Shimabukuro and Sumida 2019), 1 from the North Atlantic (Glover et al. 2005), and 1 from the Mediterranean (Taboada et al. 2015). All records are distributed from the middle to high latitudes (Rouse et al. 2018; Fujiwara et al. 2019; Shimabukuro and Sumida 2019), with a wide range of depth (21–4204 m) (Amon et al. 2014; Fujiwara et al. 2019) and a preference for low temperature (−1–15 °C) (Taboada et al. 2015). Although most *Osedax* species are known to be locally distributed, several species tend to occupy wide ocean areas. *O. deceptionensis* is found from the Antarctic to sub-Antarctic areas; *O. docricketts*, *O. randyi*, *O. roseus*, and *O. westernflyer* reside in both eastern and western sides of North Pacific (Rouse et al. 2018). Furthermore, *O. frankpressi* and *O. rubiplumus* have trans-oceanic distributions. The former was first reported from Monterey Bay, California (Rouse et al. 2004) and recently found on implanted whalebones in the Southwest Atlantic (Shimabukuro and Sumida 2019), whereas the latter is recorded from both eastern and western North Pacific and Antarctic margin (Li et al. 2017;

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Rouse et al. 2018). Despite its overall wide distribution, *Osedax* has never been reported for the Indian Ocean. The questions raised here are (1) Do *Osedax* worms occur in the Indian Ocean? If so, (2) What are their phylogenetic relationships with *Osedax* species in other oceans?

Whale bones were once experimentally deployed at two sites on the Southwest Indian Ridge (SWIR) in 2009 and were retrieved after 2-year deployment (Amon et al. 2017). However, *Osedax* worms were absent from the collections, although the deployment duration, depth, temperature, and substrates (such as whale bones) were not considered to be the limiting factors preventing their colonization (Amon et al. 2017).

In 2016, a set of culturing equipment with pig bones were deployed near Longqi hydrothermal field on the SWIR during Chinese cruise DY43. About 1 year later, *Osedax* worms were successfully captured from the bones. Here, we present the first record of *Osedax* in the Indian Ocean based on the collections from the deployment. Although morphological data is not available due to the inadequate preservation of specimens, the identification of SWIR specimens was performed using molecular evidence. In addition, the possible genetic connectivity between the Indian and Pacific oceans through the Southern Ocean is discussed.

Materials and methods

Specimen collection

Four pieces of fresh pig femur bone (about 2 kg in total) were individually drilled and then directly placed into a perspex tube (100-mm diameter × 1000-mm long). The tube, equipped with one funnel opening on one end and a cover on the other, had numerous pores (diameter 5–10 mm) on the cover and tube wall to permit water exchange (Fig. S1). Then, the package was placed in a − 80 °C lab freezer (Thermo Scientific, USA) for preservation until their deployment.

On 23 December 2016, the prepared package of bones was experimentally deployed with a mooring system on the SWIR (Fig. 3b, 49°38.685′E, 37°47.013′S, 2908 m) during the DY43 cruise of R/V *Xiangyanghong* 10. The mooring system, carrying multiple sensors (detailed in Figs. S2 and S3), was designed for the long-term observation of hydrodynamic variation on the SWIR. The deployed site is about 400 m west of Longqi hydrothermal field (Fig. 1). The tube was fixed on the mooring rope about 60 m above the ballast. On 6 January 2018, the mooring system together with the deployed bones was recovered. An SBE37 sensor (SeaBird Scientific, USA), located about 6 m above the tube, indicates a variation of water temperature from 2.18–2.24 °C and a salinity of about 34.75 PSU. After the recovery, the bones showed moderately decayed sites surrounding the drilling positions. Three *Osedax* specimens were removed from these decomposed sites and fixed in 95% (*v*/v) ethanol. Due to the paucity and low-quality of materials, it was impossible to morphologically examine the specimens and molecular analysis was conducted instead to determine species identity.

Molecular analysis

Genomic DNA extraction was carried out using Qiagen DNeasy Blood & Tissue Kit (Cat No./ID: 69504) following the procedure supplied by manufacture. Four genetic markers were amplified using Polymerase Chain Reaction (PCR): partial cytochrome c oxidase subunit I (*COI*), 16S rRNA (*16S*), 18S rRNA (*18S*), and histone H3 (*H3*) gene sequences. PCR amplifications and amplicon sequencing were performed according to the methods described in Vrijenhoek et al. (2009) and Zhou et al. (2018).

Gene sequences alignments were carried out using MUSCLE (for *COI* and *H3*) (Edgar 2004) and MAFFT (for *16S* and *18S*) (Katoh and Standley 2013). Using PAUP 4.0 (Swofford 2002), GTR-corrected distance based on COI sequences were calculated between *Osedax* species, as well as between populations of *Osedax rubiplumus*. Four datasets, *COI* (1005 bp), *H3* (370 bp), *16S* (501 bp), and *18S* (1660 bp), were used to create the final concatenated alignment (3537 bp) in SequenceMatrix 1.8. Maximum likelihood (ML) analysis was performed in IQtree 1.6.10 (Trifinopoulos et al. 2016), with evolutionary models for each partition estimated in the program automatically: TIM2+F+I+G4 for *16S*, TIM3e+I+G4 for *18S*, TVMe+I+G4 for *H3*, and GTR+F+I+G4 for *COI*. The ML bootstrap for each node was generated with an ultrafast bootstrap algorithm for 100,000 replicates.

Haplotype analysis

In order to infer phylogenetic relationships among haplotypes, a TCS network was constructed in Popart v1.7 with the addition of all *O. rubiplumus COI* sequences available in the Genbank (Clement et al. 2002; Leigh and Bryant 2015). And the only *COI* sequence from Antarctic was obtained by assembly of transcriptome data published in Li et al. (2017) (accession number: SRR3574382). A total of 99 partial *COI* sequence (about 534 bp in length) from 4 sampling localities were used in haplotype analysis (Table 1).

Results

Genetic distance and phylogeny

The new record aligns with *Osedax rubiplumus* Rouse et al., 2004, with very low divergence. The GTR-corrected distance between the new record and *O. rubiplumus* is only

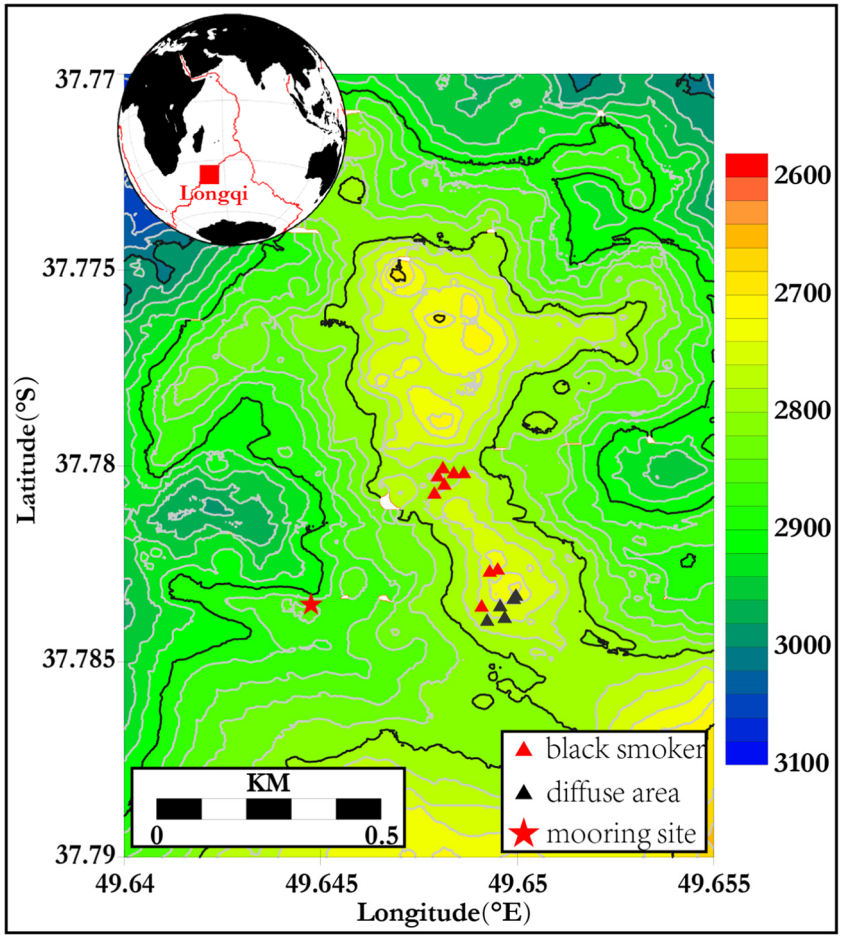

Fig. 1 Sampling location of *Osedax rubiplumus* on the SWIR and its relative position to the known venting sites at Longqi hydrothermal field. Red triangles indicate "black smokers," black triangles indicate areas with diffusing effluents, and the red star shows the mooring site

0.0091 (Table 2), which is much smaller than the inter-specific values between known *Osedax* species/OTUs (ranged 0.0705–0.2707) (Table 2) and is indicative of intra-specific divergence. This affinity is further supported by the ML tree, in which the new record clusters with *O. rubiplumus* in a branch showing extremely low divergence (bootstrap = 100). The resulting branching pattern of the ML tree reveals 6 clades (Fig. 2), the delineation of which follows those in most recent studies, despite some incongruences in terms of relative position both among and within clades (Amon et al. 2014; Fujiwara et al. 2019; Rouse et al. 2018; Taboada et al. 2015).

Within species, there are low divergences either within or between *O. rubiplumus* populations. However, the inter-ocean pairwise distances (0.0076–0.0139) are clearly higher than intra-ocean values (0–0.0036), with the largest one occurring between SWIR and Pacific sampling sites (Table 3).

Haplotype network

A total of 35 haplotypes of *O. rubiplumus* were recovered from the network analysis (Fig. 3a). Haplotypes from the Pacific formed two clusters, each with one centrally localized and dominant haplotype. The two most common haplotypes,

Table 1 Sampling information of DNA data used in haplotype analysis

No. of individuals	Sampling sites	Latitude	Longitude	Depth (m)	Accession number
1	Flanders Bay, Antarctic	− 63.166	− 65.1	700	SRR3574382
3	Longqi, SWIR	− 37.7839	49.6502	2848	MN699849- MN699851
91	Monterey Bay, California	36.708	− 122.434	1820–2890	AY586505-AY586510; EU852420-EU852488; EU223297-EU223306; EU223308-EU223311; DQ996616; DQ996620
4	Sagami Bay, Japan	35.08	139.23		FM998060-FM998063

Table 2 GTR-corrected distance (based on partial COI sequences) between *Osedax* species and OTUs

	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*O. rubiplumus* SWIR																
2	*O. antarcticus*	0.1946															
3	*O. braziliensis*	0.1797	0.1957														
4	*O. crouchi*	0.1768	0.1533	0.1982													
5	*O. deceptionensis*	0.2416	0.2257	0.2197	0.2330												
6	*O. frankpressi*	0.1873	0.2076	0.1124	0.1966	0.2154											
7	*O. japonicus*	0.1697	0.2095	0.1712	0.2051	0.2231	0.1823										
8	*O. mucofloris*	0.2226	0.2517	0.2007	0.2033	0.2424	0.2007	0.1717									
9	*O. nordenskjoeldi*	0.2066	0.1828	0.1807	0.1602	0.2310	0.1883	0.1934	0.1957								
10	*O. priapus*	0.1847	0.2071	0.1924	0.1953	0.2365	0.2040	0.1864	0.2308	0.1785							
11	*O. rogersi*	0.1934	0.1700	0.1856	0.1738	0.2477	0.1907	0.1968	0.2087	0.1737	0.1802						
12	*O. roseus*	0.1508	0.1913	0.1744	0.1860	0.2308	0.1785	0.1687	0.2039	0.2031	0.1915	0.2000					
13	*O. rubiplumus*	*0.0091*	0.2025	0.1824	0.1793	0.2427	0.1861	0.1734	0.2317	0.2067	0.1874	0.1987	0.1519				
14	*O. sigridae*	0.1755	0.2101	0.1832	0.1919	0.2094	0.1792	0.1972	0.2294	0.1768	0.1523	0.1988	0.1807	0.1743			
15	*O.* sp. MB16	0.1839	0.2390	0.1792	0.1889	0.2697	0.1868	0.1478	0.2125	0.1979	0.1753	0.1876	0.1903	0.1836	0.1999		
16	*O. bryani*	0.1689	0.2117	0.2001	0.2005	0.2245	0.2075	0.1975	0.2306	0.2062	0.2230	0.2085	0.1864	0.1638	0.1929	0.2050	
17	*O.* sp. Mediterranea	0.2081	0.2525	0.1836	0.1904	0.2334	0.2067	0.1935	0.2388	0.2064	0.1633	0.1912	0.1906	0.2110	0.1509	0.1848	0.1954
18	*O. tiburon*	0.2041	0.2142	0.1992	0.1674	0.2339	0.1925	0.2046	0.2073	0.1660	0.1868	0.1683	0.1911	0.2030	0.1821	0.2291	0.2059
19	*O. ventana*	0.1927	0.2171	0.1761	0.1718	0.2327	0.1784	0.1911	0.2240	0.1677	0.1833	0.1712	0.1847	0.1956	0.1827	0.1893	0.2155
20	*O. docricketts*	0.1826	0.2094	0.1821	0.1558	0.2433	0.1887	0.2027	0.2067	0.1836	0.1879	0.1652	0.1912	0.1828	0.1945	0.2055	0.1960
21	*O. westernflyer*	0.1936	0.2011	0.1973	0.1935	0.2273	0.2122	0.2182	0.2239	0.1838	0.2108	0.1859	0.1874	0.1926	0.1951	0.2172	0.2044
22	*O. knutei*	0.2016	0.2069	0.1937	0.1777	0.2332	0.2138	0.2167	0.1883	0.1893	0.2059	0.1786	0.2178	0.2030	0.2118	0.1878	0.2066
23	*O. lonnyi*	0.1693	0.1649	0.1831	0.1498	0.2388	0.2000	0.1936	0.2281	0.1776	0.1696	0.1370	0.1831	0.1705	0.1860	0.1826	0.1759
24	*O. packardorum*	0.1737	0.2539	0.2018	0.2146	0.2358	0.1949	0.1442	0.1793	0.2216	0.2067	0.2093	0.1824	0.1786	0.1961	0.1913	0.1917
25	*O. jabba*	0.1960	0.2362	0.1954	0.1912	0.2640	0.2034	0.1871	0.1937	0.2084	0.1862	0.2069	0.1925	0.1975	0.2014	0.2007	0.2143
26	*O. randyi*	0.1848	0.2279	0.1727	0.2088	0.2707	0.1895	0.1585	0.2091	0.2151	0.1860	0.1995	0.1954	0.1874	0.2032	0.0705	0.2046
27	*O. lehmani*	0.1764	0.2532	0.2048	0.2001	0.2264	0.1871	0.1546	0.1752	0.2241	0.1844	0.2043	0.1867	0.1774	0.2000	0.1627	0.2027
28	*O. talkovici*	0.2071	0.2584	0.2031	0.1941	0.2226	0.2031	0.1905	0.2167	0.1945	0.1962	0.1912	0.2103	0.2044	0.1869	0.2039	0.1989
29	*O. ryderi*	0.1617	0.2001	0.1941	0.1602	0.2423	0.1910	0.1809	0.2026	0.1651	0.1661	0.1657	0.1818	0.1617	0.1732	0.1742	0.2075
30	*O.* sp. sagami-3	0.1543	0.2133	0.1949	0.1864	0.2444	0.1810	0.1868	0.2179	0.1980	0.2099	0.2018	0.1625	0.1539	0.1925	0.1954	0.1839
31	*O.* sp. sagami-4	0.1240	0.1985	0.1824	0.1708	0.2678	0.1931	0.1724	0.2138	0.2001	0.1833	0.2027	0.1489	0.1272	0.1798	0.1898	0.1774
32	*O.* sp. sagami-5	0.1756	0.2211	0.1922	0.1926	0.2412	0.1961	0.1923	0.2103	0.1918	0.1634	0.1922	0.1990	0.1783	0.1145	0.2145	0.2212

Table 2 (continued)

	Taxa	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	*O. rubiplumus* SWIR																
2	*O. antarcticus*																
3	*O. braziliensis*																
4	*O. crouchi*																
5	*O. deceptionensis*																
6	*O. frankpressi*																
7	*O. japonicus*																
8	*O. mucofloris*																
9	*O. nordenskjoeldi*																
10	*O. priapus*																
11	*O. rogersi*																
12	*O. roseus*																
13	*O. rubiplumus*																
14	*O. sigridae*																
15	*O.* sp. MB16																
16	*O. bryani*																
17	*O.* sp. Mediterranea																
18	*O. tiburon*	0.1997															
19	*O. ventana*	0.2050	0.1625														
20	*O. docricketts*	0.1992	0.1695	0.1499													
21	*O. westernflyer*	0.2177	0.1902	0.1783	0.1624												
22	*O. knutei*	0.2375	0.1901	0.1858	0.1713	0.1818											
23	*O. lonnyi*	0.2029	0.1797	0.1513	0.1614	0.1812	0.1676										
24	*O. packardorum*	0.1955	0.1922	0.2148	0.1962	0.2050	0.2125	0.2037									
25	*O. jabba*	0.1992	0.1973	0.1740	0.1924	0.1991	0.1940	0.1869	0.1934								
26	*O. randyi*	0.1952	0.2248	0.2086	0.2249	0.2239	0.2035	0.1885	0.1735	0.2064							
27	*O. lehmani*	0.1927	0.1973	0.2085	0.2113	0.2198	0.1969	0.2028	0.0867	0.1965	0.1787						
28	*O. talkovici*	0.1815	0.2034	0.1997	0.1957	0.2087	0.1936	0.1967	0.1906	0.1954	0.2219	0.1856					
29	*O. ryderi*	0.2013	0.1582	0.1370	0.1569	0.1964	0.1762	0.1380	0.1908	0.1807	0.1888	0.1909	0.1868				
30	*O.* sp. sagami-3	0.2152	0.2087	0.2038	0.2096	0.1992	0.2065	0.1983	0.1774	0.2043	0.1987	0.1684	0.1885	0.1836			
31	*O.* sp. sagami-4	0.1965	0.2069	0.1914	0.1899	0.2067	0.2021	0.1683	0.1681	0.2063	0.1700	0.1797	0.2063	0.1644	0.1534		
32	*O.* sp. sagami-5	0.1596	0.1972	0.1878	0.1945	0.2008	0.2063	0.1898	0.2134	0.2026	0.2026	0.1986	0.1973	0.1860	0.2072	0.1783	

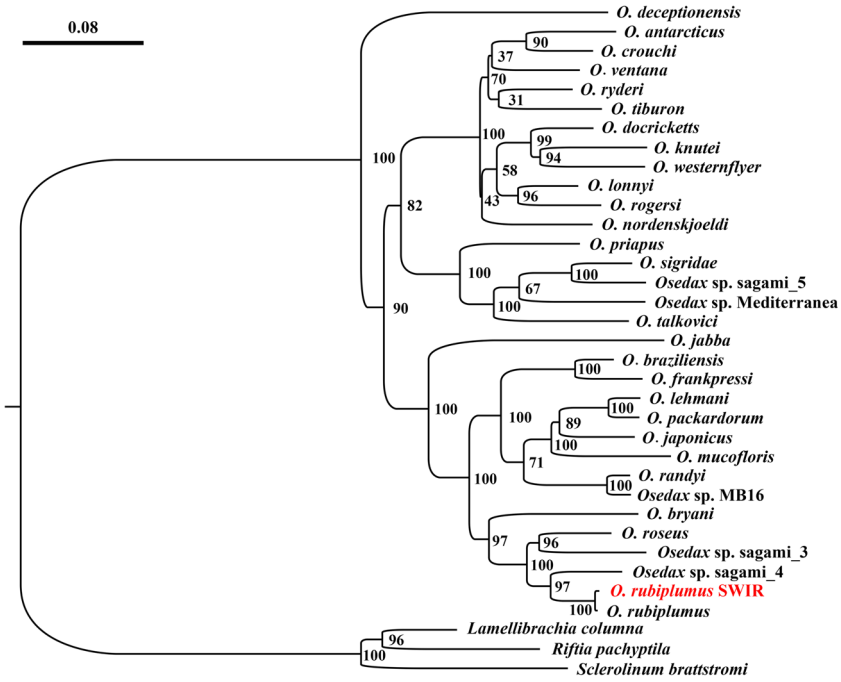

Fig. 2 Maximum likelihood (ML) tree generated from concatenated alignments of *COI*, *16S*, *18S*, and *H3*. GenBank accession numbers are listed in Table S1. Node values are bootstrap support

distinguished from each other by a single point mutation, were central to most other haplotypes, and both of them were present in both the eastern and western North Pacific. Most peripheral haplotypes were represented by one single individual and separated from the dominant ones by single substitution. Haplotypes found in Japanese waters were clustered with haplotypes from Monterey Bay, suggesting an absence of genetic structure between the eastern and western North Pacific. The three SWIR individuals were retrieved as one private haplotype, which is separated from the less dominant Pacific haplotype by six substitutions (Fig. 3a). The Antarctic haplotype appeared to be intermediately located between the Pacific and SWIR populations in the haplotype analysis (Fig. 3 a and c).

Discussion

The *Osedax* worms collected from the SWIR were genetically identified as *Osedax rubiplumus* Rouse et al., 2004, previously suggested as a widely distributed species, with occurrences in Monterey Bay, Sagami Bay, and the Antarctic margin, with a depth range of 700–2890 m (Li et al. 2017; Rouse et al. 2018; Smith et al. 2015). Thus, our result expanded its known range to the Indian Ocean, revealing a much larger range of *Osedax* species than previously reported.

The trans-oceanic distribution of *O. rubiplumus* indicates that it is capable of long-distance dispersal, which is further supported by its large larval size (Rouse et al. 2009). There are two passages of water exchange between the Pacific and Indian oceans, the Indonesian Throughflow and the Southern Ocean. The first is limited to shallow waters, which is unlikely to be the "highway" of larval dispersal as the high temperature of the water column might prevent the invasion of *Osedax* (Rouse et al. 2009; Amon et al. 2014). In contrast, the Antarctic Circumpolar Current (ACC) has been proposed to be responsible for the recent or ongoing trans-oceanic dispersal for some deep-sea taxa, such as *Kiwa* crabs and *Neolepas* stalked barnacles (Roterman et al. 2013; Watanabe et al. 2018), due to the genetic affinities between the populations in the Southern Ocean and Southwest Indian Ocean. Among the three *O. rubiplumus* populations, the greatest genetic difference is found between the populations in the Pacific Ocean and the Southwest Indian Ocean, whereas the Antarctic individuals show higher genetic similarity with both. Although without strong support due to the small sample size in the Antarctic and Southwest Indian oceans, the most plausible explanation to the present distribution pattern is that the Antarctic acts as one of the "stepping stones" connecting the Pacific and Indian

Table 3 GTR-corrected distances between sampling localities of *Osedax rubiplumus*

	Sampling sites	1	2	3	4
1	Monterey Bay, California	0.0036			
2	Sagami Bay, Japan	0.0022	0.0009		
3	Flanders Bay, Antarctic	0.0101	0.0090	0	
4	Longqi, SWIR	0.0139	0.0128	0.0076	0

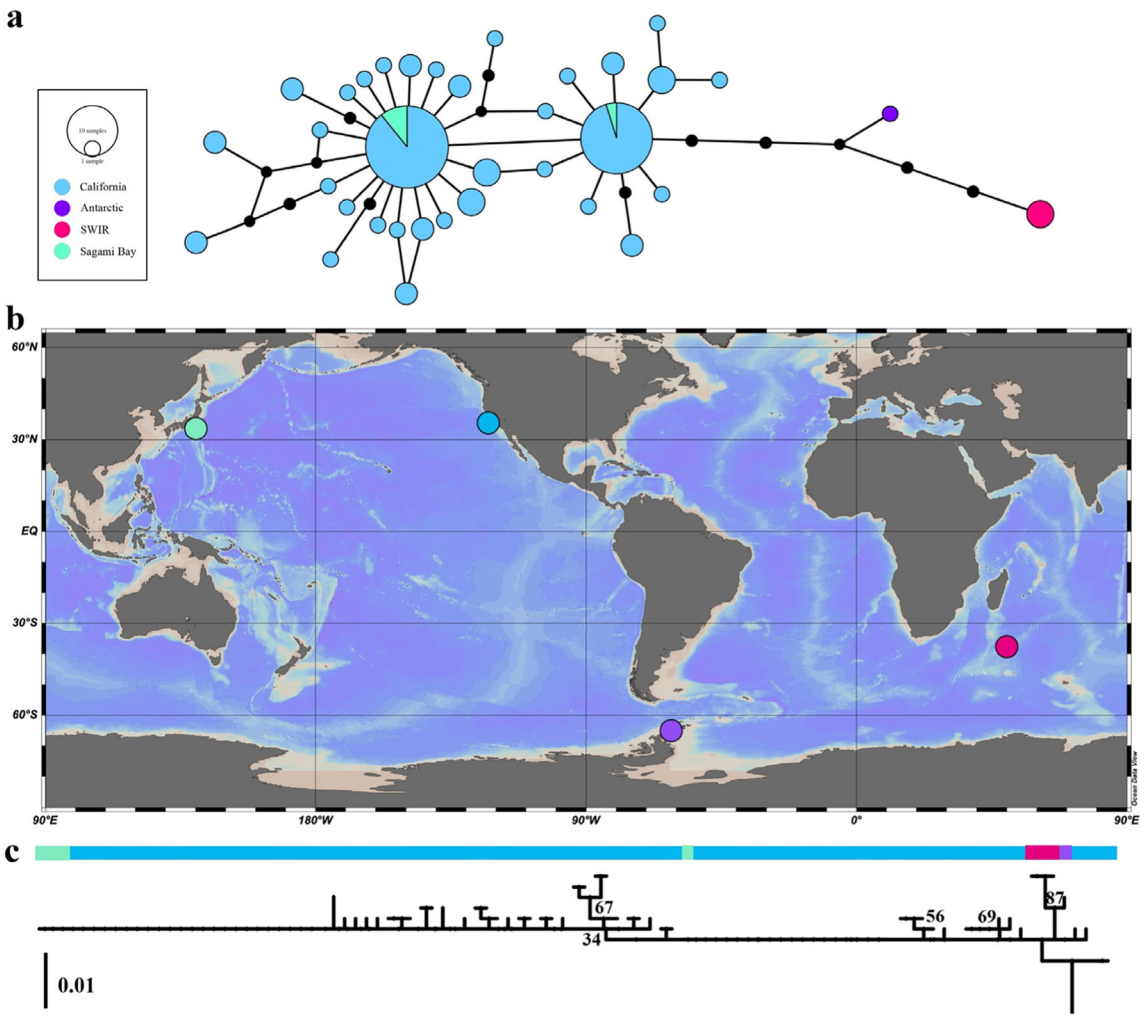

Fig. 3 **a** Haplotype network constructed using the partial *COI* sequences of *O. rubiplumus* sampled from California (dark blue), Sagami Bay (light blue), Antarctic (purple), and SWIR (red). Each black dot indicates one missing haplotype, and each line indicates one substitution; **b** Locations of *Osedax rubiplumus* populations analyzed in the present study (in the same color style as **a**); **c** ML tree showing phylogenetic relationships among *COI* haplotypes of *O. rubiplumus*, with *Osedax* sp. Sagami_4 as the outgroup. Bars indicate haplotype groups and are colored according to their locations. Numbers at some nodes indicate bootstrap values

Ocean populations. Given the high abundance of whales and other large marine mammals in the Southern Ocean, substrates formed by mammal carcasses and suitable for *Osedax* colonization, are anticipated to be widespread surrounding the Antarctic (Amon et al. 2014). These hospitable habitats are capable of hosting large *Osedax* populations (Amon et al. 2014), supporting them to travel in the Southern Ocean, and expanding their range across oceans. Similarly, the capability of long-distance dispersal resulting from large female and oocytes, together with the small distance between natural whale falls (estimated for nine gray whale species in Smith and Baco 2003), may also explain the inter-basin distribution of *O. frankpressi* (Shimabukuro and Sumida 2019).

Haplotype network shows signals of three distinct clusters in the Pacific, Antarctic, and Indian oceans, respectively. The divergence among the three oceans might be attributed to the latitudinal fluctuation of ACC, which would influence the degree of connectivity between the Antarctic and the other oceans (Roterman et al. 2013; Dueñas et al. 2016). On the other hand, the ACC is considered to be a semi-permeable barrier due to its thermal isolation from the surrounding waters and only permit limited gene flow, resulting in a bottleneck event and separating populations for some deep-sea fauna (Dueñas et al. 2016; Georgieva et al. 2015). The large geographic distance is likely to strengthen those effects (Shimabukuro and Sumida 2019). However, given the high level of haplotype diversity and divergences reported for other *Osedax* species (Amon et al. 2014; Taboada et al. 2015) and the lack of *O. rubiplumus* data from the Antarctic and Indian oceans, our results should be interpreted with caution. More individuals and populations are needed to test the above-mentioned scenario.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgments, if applicable.

Data availability The datasets generated and/or analyzed during the current study are available in the GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/).

Author contribution CW conceived the research. YZ, YW, ZL and CS designed this research. YW and CS carried out the field experiment. YZ, YW and YL analyzed the data. YZ, YL, ZL and CW wrote the manuscript. All of the authors read and approved the manuscript.

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