Ephemeral Occurrence of the Echiuran *Listriolobus brevirostris* (Annelida: Echiura) in Osaka Bay between 1995 and 2002; a New Record for Japan, Probably Resulting from Human-mediated Introduction

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The primarily Indo-West Pacific echiuran *Listriolobus brevirostris* Chen and Yeh, 1958 was collected, sometimes abundantly, from benthos samples from northeastern Osaka Bay (from 6.4–17.5 m depth) between 1999 and 2001, or recorded in the field between 1995 and 2002. Since 2003, it has remained uncollected. These records were shown to represent the first occurrence of *L. brevirostris* in Japanese waters, being the first reliable evidence so far determined of the introduction of an exotic echiuran species, probably in ballast water, to any locality worldwide. Aquarium observations suggested a completely infaunal adult life mode, including feeding activity. Monthly changes in size distribution of specimens collected in 1999 indicated successful summer survival under oxygen-depleted bottom conditions in Osaka Bay. Factors behind the ephemeral occurrence of *L. brevirostris* in Osaka Bay were briefly considered in relation to annual fluctuations of dissolved oxygen content in bottom water, although the driving forces behind such occurrence remain to be established.

**Key Words:** Alien species, ballast water, ephemerality, oxygen-depleted bottom.

Introduction

Invasive benthic populations may be often unstable, even disappearing after only a few generations following colonization. Ephemeral occurrences of alien species in Japan include a single record of a European ascidian, *Ascidiella scabra* (Müller, 1776), 18 individuals of which were collected (probably in 1861) from Nagasaki (Nishikawa and Otani 2004), and an exotic barnacle, *Amphibalanus venustus* (Darwin, 1854), recorded in Japanese waters only in 1967 and 1968 (Iwasaki et al. 2004). The current report of the primarily Indo-West Pacific echiuran *Listriolobus brevirostris* Chen and Yeh, 1958 (Figs 1, 2) appears to be a further example. It was collected among benthos samples (voucher specimens) from northeastern Osaka Bay between 1999 and 2001, or recorded in the field between 1995 and 2002 (field notes only taken), as an echiuran new to Japanese waters, and has remained uncollected since 2003. Such a recent and isolated discovery in an international harbor area such as Osaka Bay is likely attributable to human-mediated introduction, rather than to a natural expansion of the species’ distribution. Accordingly, the report of *L. brevirostris* from Osaka Bay may be the first reliable indication of an invasive introduction of an exotic echiuran species to Japan. Taxonomic and biological accounts of the population are given below, and the causes of ephemerality of the Osaka Bay population briefly considered.

Fig. 1. Photograph of a living individual of *Listriolobus brevirostris*, dredged on 18 August 1999 in the northern end of Osaka Bay, Japan (NSMT-Ec 165). Scale bar: 1 cm.

Fig. 2. Map showing the only known localities of *Listriolobus brevirostris*, each with earliest recorded year(s) of occurrence (see text).
Materials and methods, and Survey Results

Most of the echinuran material was collected by I. A. during benthos surveys off Kobe, Amagasaki, Ashiya and Osaka Cities in the northeastern part of Osaka Bay, organized by the Osaka Port Development and Engineering Corporation (for details see Osaka Port Development and Engineering Corporation 2000). Fifteen surveys were conducted on the muddy bottom (silt, 60–80%; clay, 20–40%) (each taking a full day) on 29 April, 10 May, 3, 8, and 23 June, 6 and 21 July, 5 and 18 August, 2, 13 and 27 September, 13 and 26 October, and 23 December in 1999, using net dredges with a 3 mm mesh net. Eleven surveyed stations were fixed with a stone-weighted entrance frame and a series of digging claws (called “Ishigeta-ami” in Japanese), further covered with a 3 mm mesh net. Density calculated on basis of dredged bottom area measured at each station for each survey (individual survey area not shown).

Additional specimens, collected from Osaka Bay in 1999 to 2001 for taxonomic purposes, are deposited in NSMT and the Osaka Museum of Natural History (OMNH) (see below).

To understand some of the possible factors related to the ephemeral occurrence of *Listriolobus brevirostris*, annual fluctuations in the minimal content (in mg per litter) of dissolved oxygen (DO) of bottom water, 1 m above the bottom surface, were examined. Monthly DO data for Osaka Bay from 1983 to 2016 were obtained from the Research Institute of Environment, Agriculture and Fisheries, Osaka Prefecture websites (1983–2005, http://www.kannousui-ken-osaka.or.jp/publication/suisan_jigyo/index.html; 2006–2016, http://www.kannousui-ken-osaka.or.jp/publication/suisan_shiryo/index.html; both accessed on 27 December 2018), the data having been routinely collected during a “Monitoring Program of Water Quality in Fishing Grounds of Osaka Bay” by the Fisheries Experimental Station of Osaka Prefecture and its successor, the Research Institute of Environment, Agri-

| Table 1. Numbers and densities of *Listriolobus brevirostris* at 11 stations during 15 surveys in 1999 in Osaka Bay, with station data (for details see text). Density calculated on basis of dredged bottom area measured at each station for each survey (individual survey area not shown). |
|----------------------------------------|-----------------|----------------|----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Date of survey in 1999                | Number of individuals (density, m⁻²) |
|----------------------------------------|--------------------------------------|
| Station data                           | Stn 2       | Stn 5       | Stn 7       | Stn 9       | Stn 10       | Stn 20       | Stn 22       | Stn 26       | Stn 34       | Stn 37       | Stn 41       |
| Latitude, Longitude (WGS84-based)      | 34°41.2′N | 34°40.9′N | 34°40.0′N | 34°40.1′N | 34°40.0′N | 34°37.9′N | 34°38.0′N | 34°36.9′N | 34°35.8′N | 34°35.2′N | 34°34.4′N |
| Depth                                  | 10.5 m     | 4.5 m      | 15.2 m     | 13.1 m     | 10.1 m     | 13.4 m     | 9.1 m      | 17.1 m      | 9.1 m      | 12.4 m      | 6.4 m       |
| Dredged area                           | 50–430 m² | 60–520 m² | 140–440 m² | 170–950 m² | 90–560 m² | 90–740 m² | 90–560 m² | 260–850 m² | 280–950 m² | 230–950 m² |
| 29 April                               | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 10 May                                 | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 3 June                                 | 0          | 0          | 0          | 0          | 1 (0.007) | 0          | 0          | 0          | 0          | 0          | 0          |
| 8 June                                 | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 23 June                                | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 6 July                                 | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 21 July                                | 0          | 0          | 14 (0.002) | 0          | 0          | 0          | 0          | 0          | 1 (0.001) | 8 (0.009)  | 0          |
| 5 August                               | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| 18 August                              | 0          | 0          | 6 (0.032)  | 2 (0.003)  | 0          | 0          | 0          | 0          | 0          | 1 (0.001)  | 0          |
| 2 September                            | 0          | 0          | 2 (0.009)  | 1 (0.001)  | 0          | 0          | 0          | 0          | 0          | 2 (0.003)  | 1 (0.002)  |
| 13 September                           | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 1 (0.001)  | 0          |
| 27 September                           | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 1 (0.001)  | 0          |
| 13 October                             | 0          | 0          | 5 (0.025)  | 1 (0.001)  | 0          | 0          | 0          | 0          | 0          | 1 (0.002)  | 1 (0.001)  |
| 26 October                             | 0          | 0          | 3 (0.018)  | 121 (0.170)*| 0          | 0          | 0          | 0          | 3 (0.005)  | 0          |
| 23 December                            | 0          | 0          | 4 (0.016)  | 0          | 0          | 0          | 0          | 0          | 0          | 2 (0.003)  | 1 (0.001)  |

* indicates specimens (21 of 121) fixed for morphological studies.
First Japanese record of *Listriolobus brevirostris*  

Culture and Fisheries, Osaka Prefecture. The data for each year comprised monthly measurements at 15 fixed stations (one station of only 6 years’ duration subsequently omitted here) established in the eastern half of Osaka Bay, the latter with far less oxygenated bottom conditions than in the western half (Fujiwara et al. 2004; Akiyama 2015); among them, Stns 13, 14, 15, 16, 17, and 18, located at the northeastern end of the bay, were closely comparable to the echinuran-collected stations of the "Ishigeta-ami" survey (above) and were therefore considered representative of *L. brevirostris* habitat. The "minimal DO month", defined here as the lowest average of DO measurements over the 14 stations, varied each year [June (rarely), July, August, or September]. For each "minimal DO month" of each year, the average DO contents of Stns 13, 14, 15, 16, 17, and 18 were calculated and regarded as the minimal DO content of each respective year for actual or potential echinuran habitat, the average over the remaining 8 stations being used for comparison. Data was unavailable for Stn 18 in 2010.

**Taxonomy**

**Genus** *Listriolobus* Spengel, 1912

**Diagnosis**  
[based on Nishikawa (2004); emended by Tanaka et al. (2014)]. Longitudinal muscle of body wall grouped into bands (at least in adults); inner-most oblique muscles continuous, never separated into fascicles between longitudinal muscle bands; one to three pairs (often with some anomalies) of gonoducts, their gonostomes located proximally; gonostomal lips elongated, often coiled spirally; interbasal muscle present or absent; rectal caecum present.

**Listriolobus brevirostris** Chen and Yeh, 1958  
(New Japanese Name: Minato Tatejima Yumushi)  
(Figs 1–5; Table 1)

*Listriolobus brevirostris* Chen and Yeh, 1958: 269–270, 276–278, text-figs 5–7; Stephen and Edmonds 1972: 424; DattaGupta and Menon 1966: 193–195, text-fig. 1A, fig. 2A; Edmonds 1987: 131–132, text-figs 12–13, 22; Li et al. 1994: 206; Wang et al. 1995: 31; Halder 2004: 253; Zhou et al. 2007: 147–149, text-fig. 85; Al-Yamani et al. 2012: 114, pl. 77.

*Listriolobus bulbocaudatus* Edmonds, 1963: 243–245, pl. 1, fig. 1; Stephen and Edmonds 1972: 423.

*Listriolobus aff. bulbocaudatus*: Al-Yamani et al. 2009: 25.

**Material Examined.** Specimens serially dredged in northeastern Osaka Bay in 1999, 6.4–15.2 m deep, fixed in formalin or Bouin’s fluid (abbreviated as B-fixed), collected by I. A. (station data given in Table 1). Registered as NSMT-Ec: 186, A. anterior end of trunk; B. posterior end of trunk (ventral vessel undetectable due to deterioration). Abbreviations: al, alimentary canal; av, anal vesicle; dv, dorsal vessel; gd, gonoduct; gl, gonostomal lip; im, interbasal muscle; nv, neurointestinal vessel; rc, rectal caecum; re, rectum; rv, ring vessel; tb, terminal bulb; vn, ventral nerve cord; vs, ventral seta; vv, ventral vessel. Scale bars: 1 mm.

3 inds; 177, 26 October, Stn 7, 2 inds; 178, 26 October, Stn 9, 21 inds; 179, 26 October, Stn 37, 2 inds; 180, 23 December, Stn 7, 4 inds, B-fixed; 181, 23 December, Stn 34, 2 inds, B-fixed; 182, 23 December, Stn 37, 1 ind., B-fixed; 183, 23 December, Stn 41, 1 ind., B-fixed; 184, Near “Kobe Port Island”, Kobe, Osaka Bay, 28 October 1999, M. Otani coll., 1 ind. OMNH-Iv 1820, Off “Kobe Port Island”, Kobe, Osaka Bay, 17.5 m deep, 4 November 1999, M. Otani coll., 1 ind., 186, Off Kobe, Osaka Bay, 26 November 2001, M. Otani coll., 1 ind. OMNH-Iv 1820, Off “Kobe Port Island”, Kobe, Osaka Bay, 19 December 2000, M. Hanaoka coll., 48 inds; 4488, Off Sakai, Osaka Bay, 1 March 2000, H. Ariyama coll., 6 inds.

**Description.** In larger living specimens, trunk predominantly light or dark reddish with narrow white longitudinal lines representing muscle bands, posterior end usually opaque and white due to thick fleshy wall forming a coni-
cal terminal bulb; proboscis white to pale yellow, with nearly smooth deeper yellow edges. Reddish trunk coloration and white terminal bulb inconspicuous in smaller specimens. Proboscis 1.7–16.0 mm long, ranging approx. 4–28% (20% in average) of total body length (7.3–136.5 mm) in 52 fixed complete specimens (proboscis/trunk length proportion variable, see Fig. 4); edges separated completely to mouth level, weakly or deeply undulating due to shrinkage at fixation. Trunk cylindrical, up to 124.5 mm long; its surface densely covered with round (sometimes conical at anterior extremity) papillae, up to 0.2 mm high, mostly arranged annularly. Anterior end of terminal bulb fringed with a prominent ring of wart-like papillae, sometimes up to 0.3 mm high (Fig. 3B). Seven longitudinal muscle bands. One pair of ventral setae, their distal one-fourth sickle-shaped; interbasal muscle present. Two pairs of gonoducts posterior to ventral setae; gonostomes proximal, lips elongated and spirally coiled (Fig. 3A). Gonoducts usually small, empty [somewhat elongated and filled with eggs or opaque white matter (sperm?) in specimens collected in August and early September (see Fig. 5)]. Neurointestinal vessel issuing from ventral vessel (running along ventral nerve cord), forming a very narrow loop around interbasal muscle, subsequently dorsally bifurcated and terminating on each side of ring vessel (Fig. 3A). Rectal caecum present, but its connection with deteriorated ventral vessel unrecognizable. Paired anal vesicles, probably free (without mesenteries), but too damaged for detailed description.

Remarks. The present descriptions were very similar to previous descriptions of *L. brevirostris* in having a very short proboscis, trunk terminal bulb, 7 longitudinal muscle bands, sickle-shaped ventral setae, interbasal muscle, two pairs of postsetal gonoducts, orientation of the neurointestinal vessel, and presence of a rectal caecum. Edmonds (1963) distinguished his newly-established *L. bulbocaudatus* from *L. brevirostris* by the presence (in the former) or absence (in the latter) of the terminal bulb, but later (Edmonds 1987) found the bulb to be sometimes undetectable among specimens from the type locality of the former species (Queensland, Australia), and concluded that the two species were conspecific (*L. brevirostris* having priority). *Listriolobus brevirostris* is clearly distinguishable from the 5 congeners so far known (see Nishikawa 2004: table 3), including the only known Japanese congener *L. sorbullians* (Lampert, 1883). The latter differs markedly from the Japanese specimens of *L. brevirostris* in the relative length of the proboscis (from 15% to more than 50% in the former vs. 4–28% in the latter), and in having usually 3 pairs of gonoducts (vs. 2), 11–16 longitudinal muscle bands (vs. 7), and the interbasal muscle absent (vs. present). On the basis of previous descriptions and his examination of a paratype of *Thalassema arkati* Prashad, 1935, Nishikawa (2004) suggested the possible conspecificity of *L. brevirostris* with *T. arkati* (type locality: Kolkata, India), given as *Ochetostoma arkati* by Biseswar (1988), and *L. capensis* (Jones and Stephen, 1955) (South Africa), both with seven or eight longitudinal muscle bands and two post-setal pairs of gonoducts. Further, *T. arkati* was originally described as having structure similar to the terminal bulb in *L. brevirostris* (see Prashad 1935: pl. 1, fig. 1), although the above-referred paratype lacked it (Nishikawa, unpublished). Such a terminal structure has been reported also in South African specimens of *O. formosulam* (Lampert, 1883) by Biseswar (1988), and in the original descriptions of *O. septenytom* DattaGupta, Menon, and Johnson, 1963 (from Quilon, SW coast of India) by DattaGupta et al. (1963), and *Anelassorhycthus dendarhynchus* (Annandale and Kemp, 1915) (from Chilka Lake, E coast of India) by Annandale and Kemp (1915), though these generic affiliations do not seem to be firmly established to date. Morphological and molecular characteristics should be further addressed in future taxonomic revisions of *L. brevirostris* and its allies. Until then, the above-stated conspecificity remains unacceptable.

Among previous descriptions of *L. brevirostris*, DattaGupta and Menon (1966) provided the only account of mature specimens, collected in April, 1963 from Kerala, India. In the present study, mature specimens were collected in August and early September. Further collections of mature *L. brevirostris* from additional localities should cast more light on the biology of the species.

Geographical Distribution. See Fig. 2: Osaka Bay, Osaka, Japan, 6.4–17.5 m deep, mud (present study); Bohai Bay (Peng et al. 2013; Xiong et al. 2014; Wu et al. 2014), Xiaochow (=Jiaozhou) Bay, Shangtung (Chen and Yeh 1958; Zhou et al. 2007), Liyuan (=Jiangsu) Bay, Jiangsu (Chen and Yeh 1958), Haimen Bay, Guangdong (Li et al. 1997), Daya Bay, Guangdong (Du et al. 2011; Zhang et al. 2017; Chen et al. 2019), and Baimajing, NW Hainan (Li et al. 1994; Zhou et al. 2007), China; Hong Kong (Kwok et al. 2008 based on Shin et al. 2004; Wang et al. 2017); Moreton Bay, Queensland, Australia, 8–10 fathoms (Edmonds 1963); Yeppoon, Hervey Bay, and Bramble Bay, Queensland, Australia, mud (Edmonds 1987); Cochin (=Kochi), Kerala, India (DattaGupta and Menon 1966); Shivaraipur, Gujarat, India (Halder 2004); Kuwait Bay, Kuwait, Kuwait, 12 m (Al-Yamani et al. 2009).
Behavioral Observations and Discussion

Adult infaunal life mode. The aquarium observations during the present study included the following: (1) when placed very gently on the mud surface, adult *Listriolobus brevirostris* expanded and contracted repeatedly, digging into the mud from its posterior end; (2) from within the mud, each individual (probably with the anus upward) periodically emitted numerous minute fecal pellets from the burrow opening; (3) the “mountain” so-formed and burrow seemed to be stable since the surface of both had begun pale (due to oxidation) within two days; (4) the proboscis was undetectable on the mud surface; (5) the burrow appeared to have a single opening at the center of the “mountain”. These observations indicated that *L. brevirostris* at no time scoops mud (with detritus) from the substrate surface by extending its proboscis from the burrow, as done by many other echiurans. Instead, the short proboscis may possibly be utilized for making a burrow, thereby ingesting substratum material. It follows that *L. brevirostris* adults may have a completely infaunal life mode, although this consideration is based on very limited observations.

Life history in Osaka Bay. Figure 5 shows that *L. brevirostris* in Osaka Bay matured in August and early September, the larger spawned individuals probably dying thereafter. A new generation was recruited from August to October with the settlement of pelagic larvae, growing to maturity by the next summer, probably with a single year longevity. Figure 5 clearly shows that juveniles and adults together survived the oxygen-depleted or even anoxic bottom environment during summer (see Yamochi et al. 1998). Yamochi et al. (2001) indicated that their “Class Echiura species” (identified here as *L. brevirostris*) was the second or third dominant benthic species by individual number in summer, based on the results of the “Ishigeta-ami” benthos survey in 1999.

First occurrence of *L. brevirostris* in Japan. Prior to the present account, *L. brevirostris* had not been recorded from Japanese waters, although the possibility cannot be ruled out that this subtidal infaunal species had remained uncollected since the beginning of echinuran taxonomy in Japan around 1900. Sato (1934) described some echiurans from Onomichi Bay, Seto Inland Sea, adjacent to Osaka Bay, but none reminiscent of *L. brevirostris*. Although comprehensive benthos surveys in Osaka in 1937, 1938 and 1939 by Miyadi (1938, 1940a, b), and in 1983 (Yamanishi 1988, 1990) included detailed reports on megalo- and macrobenthic fauna, the earliest record of an echinuran from the bay was that of Yamochi et al. (1998, table 3), who listed specimens of “Urechis unicinctus” collected in August 1995. However, according to one of the authors of the list, Dr. H. Ariyama (pers. comm. to T. N., 16 June 2008), the identification was incorrect, the specimens instead being referable to *L. brevirostris*, with which they shared similar external features. Although the listed specimens are now unavailable, their subsequent identification is supported here by the *L. brevirostris* specimens (registered as OMNH-Iv 4488) collected by Dr. Ariyama (see “Taxonomy” section above). Accordingly, *L. brevirostris* can be considered as having been present in Osaka Bay no later than 1995. In fact, an earlier occurrence may be possible, because Joh et al. (1969) recorded unidentified echinuran specimens in the inner part of Osaka Bay, mainly from off Kobe, Osaka, and Sakai Cities, 10.0–20.0 m deep, in the autumn of 1968, and Nishi et al. (1998) also recorded “Phylum Echiura indet.” from the outer-most part of the bay, 60 m deep, in 1993 and/or 1996, both using S–M samplers. Unfortunately, however, neither these specimens nor field photographs are now available, making their specific identification impossible.

Natural or human-mediated introduction? A few species of echinurids are known to have planktotrophic larvae capable of surviving up to 50 days (Newby 1940; Sakiyama 1958). While this pelagic larval life length could conceivably permit transport from Chinese coastal waters in Kuroshio Current (but likely being far too short of a planktonic life to permit transequatorial transport from Australia), we suggest that the very recent and isolated occurrence in Osaka Bay seems more likely to have resulted from human-mediated introduction, possibly to one of the five international ports in the Bay (Osaka, Kobe, Sakai-Senboku, Han-nan,

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**Fig. 5.** Seasonal changes in trunk length of *Listriolobus brevirostris* from Osaka Bay in 1999. Solid bars indicate mature specimen(s), dotted lines, measurements from live specimens, and double-headed arrow of dotted line, the length range in live specimens (see text).
and Amagasaki-Nishinomiya-Ashiya Ports). Osaka Bay has been documented as the Japanese gateway for the invasive European mussel *Mytilus galloprovincialis* Lamarck, 1819 (close to Kobe Harbor in 1932; see Iwasaki *et al.* 2004), in addition to more than 10 other exotic marine animals (see Nabeshima 2002). Containment in the ballast water of international ships is the most likely mechanism for human-mediated translocation of many soft-bottom benthic marine organisms, such as *L. brevirostris* (see Otani 2004: table 1), due to the species’ fragile and easily abraded skin, inability to attach to a hard substratum (*e.g.*, hulls), infaunal adult life mode, and likely long larval duration (as is usual in echiurids). Although zooplankters (*including* pelagic larvae) in ballast water are unlikely to survive 16-day-long transoceanic Atlantic transportation (Wotham 2001), the likelihood of survival may increase for shorter trips, *e.g.*, from northern China to central Japan. This consideration may bear weight due to the species’ other localities (see Fig. 2), including Cochin, western India and Kuwait Bay, both with large international ports. Notwithstanding, nothing is known, in fact, about larval duration and survival in *L. brevirostris*. It remains, however, that the Japanese records of *L. brevirostris* probably represent the first known exotic occurrence of an echiuran species.

**Fluctuations of the Osaka Bay *L. brevirostris* population in oxygen-depleted bottom water.** While working for the Osaka Prefectural Fisheries Experimental Station and its successors, Dr. Ariyama (pers. comm. to T. N., 16 June 2008) performed routine benthos surveys in Osaka Bay from November 1993 to June 2003, up to 4 times per year (1993–1996), in depths ≤ 10 m, mainly using "Ishigeta-ami". Echiuran specimens, now identifiable as *L. brevirostris*, were collected only in inner parts of the bay, off Kobe to Sakai Cities, from August 1995 to August 2002, the highest yield being 73 individuals in July 2002. The detailed records made at the time support the conclusion that *L. brevirostris* occurred in the inner part of Osaka Bay from August 1995 to August 2002. Additional information was obtained from the results of the "Macrobenthos Monitoring Project" in Osaka Bay, performed every year in May and October from 1990 to 2016 using an S-M sampler (covering 0.1 m²) primarily at five fixed stations, three of which were located in the inner part of the Bay, available from the Research Institute of Environment, Agriculture and Fisheries, Osaka Prefecture websites (1990–2005, http://www.kannousuiken-osaka.or.jp/publication/suisan_jigyo/index.html; 2006–2016, http://www.kannousuiken-osaka.or.jp/publication/suisan-shiryo/index.html; both accessed on 15 March 2018). The results showed that "Echiuroidea sp." were collected only in October 1998 (one individual from off Sen’nan City, ca. 13 m deep) and May and October, 1999 (one and seven, respectively, from the central part of the bay, 34 m) between 1990 and 2016; these records are closely reminiscent of the simultaneous occurrences of *L. brevirostris* in the Bay, as reported here. Thus, it may be concluded that *L. brevirostris* has been uncollected after August 2002 from that area. Such a decline was also reported by Stull *et al.* (1986) for an indigenous population of a congener, *L. pelodes* Fisher, 1946, off California, U. S. A., around 60 m deep, after flourishing between 1972 and 1977, although the cause was unknown. In contrast, Zhang *et al.* (2017) reported the occurrence of *L. brevirostris* almost every year between 2004 and 2015 (excepting 2006 and 2007) in Daya Bay, Guangdong, China, based on the results of summer trawling surveys, and supplemented by others in spring and autumn. Density varied during the period, ranked as high as "second dominant species" in 2013 and "dominant species" in 2004 and 2014, the causes of the fluctuations being unknown.

Nabeshima (2002) suggested that extreme oxygen-depleted bottom water in summer resulted in a decrease in indigenous species, whilst giving exotic species a greater opportunity to survive. This does not seem applicable in the present case, judging from Fig. 6, which clearly shows that throughout the period analyzed, the annual minimal DO content in the *L. brevirostris*-inhabited area was invariably well below 3 mg/L and regarded as oxygen-depleted (see, *e.g.*, Fujiwara *et al.* 2004), and lower than in the non-resident area each year, indicating that the echiuran can persist in an oxygen-depleted environment. Such ability, especially in pelagic larvae and settled juveniles in summer, must be a key advantage in invading and colonizing the northeastern end of Osaka Bay, which is extremely oxygen-depleted in summer. However, Fig. 6 indicates no causal relationship between the annual fluctuation pattern of minimal DO content in the *L. brevirostris*-inhabited area and the very limited occurrence of the species from 1995 to 2002. Before 1995, the bottom

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**Fig. 6.** Annual fluctuations in minimal dissolved oxygen content (mg/L) of the bottom water layer in the most oxygen-depleted (eastern) portion of Osaka Bay. Solid line indicates data from area formerly inhabited by *Listriolobus brevirostris* (northeastern Osaka Bay); dashed line indicates data from area devoid of *L. brevirostris* (remaining eastern portion of Osaka Bay).
water had been oxygen-depleted (see above), decreasing repeatedly to extremes of 1 mg/L or less, resulting in the likely disappearance of "indigenous species" sensu Nabeshima (2002) before 1995. However, a similar disappearance of the echiuran population cannot be attributable to extreme oxygen-depletion, because it survived such conditions in 1999. Accordingly, the driving forces behind the ephemeral occurrence of *L. brevirostris* remain to be established. If larval recruitment in ballast water is a factor, *L. brevirostris* may settle again in Osaka Bay in the future, or in fact, in some other international port regions, characterized by oxygen-depletion in summer, in Japan or elsewhere.

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