1 **Facultative commensalism of free-burrowing, urothoid amphipod with deep burrow-dwelling**

2 **callianassid shrimp on an intertidal sandflat**

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25 **Abstract**

26 Species of the free-burrowing amphipod genus, *Urothoe*, are common macrobenthos on open sandy

27 beaches. On intertidal sandflats, some species are associated with burrows or tubes of large infauna.

28 How this link is formed under sheltered settings was examined. On an intertidal sandflat emersed for

29 300 m seaward in mid-western Kyushu, Japan, *U. carda* co-occurred with the deep burrow-dwelling

30 callianassid shrimp, *Nihonotrypaea harmandi*. Amphipods resided in the surface 5-cm sediment

31 outside shrimp burrows, as confirmed by sediment coring and burrow casting. In the summertime

32 during 1980 to 1981, the shrimp and amphipod populations were confined to the upper shore at

33 mean densities of 182 and 701 inds m^{-2}, respectively. In winter to spring, when the sediment surface

34 mixing was caused by seasonal wind-induced waves, only the amphipod extended distribution to the

35 lowest shore. By 1983, the shrimp increased mean density by 2.5 times and distribution range to the

36 lowest shore. In the summers of 1984, 2010, and 2015, the amphipod extended distribution to the

37 lowest shore, with small variations in population size. Three marked changes in substrate properties

38 were associated with the shrimp inhabitation: thicker oxidized layer (proxy for oxygenated layer) in

39 the sediment column; looser surface sediment, as evaluated with vane shear strength; and coarser

40 and better-sorted surface sediment with less mud content. At least the former two changes were

41 attributable to shrimp bioturbation, which could provide the amphipod with more permeable and

42 softer substrates, leading to the formation of facultative commensalism.

43

44 **Introduction**

45   Species of the gammaridean amphipod genus, *Urothoe*, are cosmopolitan members of the benthic

46 macro-infauna on open sandy beaches and shallow subtidal sandy bottoms (Bousfield 1970; Bally

47 1983; Barnard and Karaman 1991). Their high burrowing ability is an adaptation to shifting

48 sediment, with broad-fusiform body form believed suited to filter-feeding in loosely packed sand

49   (Bousfield 1970). Among the free-burrowing amphipods, adults of *Urothoe* spp. reside relatively

50   deep in the sediment (Vader 1978; Sudo 1988). *Urothoe* spp. also occur as surf plankton (Fincham

51   1970; Yu et al. 2002), with males performing nocturnal excursions into the water column probably as

52   a part of mating behavior (Fincham 1970; Sudo 1988; Fernandez-Gonzalez et al. 2014). Some

53   species of *Urothoe* inhabit intertidal sandflats that are more sheltered than open sandy beaches. On

54   sheltered habitats, individuals of some *Urothoe* spp. are associated with deep burrows or tubes of

55   much larger-bodied infauna such as ophiuroids, spatangoid echinoids, and an apodid holothuroid

56   (Vader 1978), an arenicolid polychaete (Lackschewitz and Reise 1998), and a terebellid polychaete

57   (Callaway 2006). Individuals of these *Urothoe* spp. dwell inside (Vader 1978; Lackschewitz and

58   Reise 1998) and/or closely outside (Vader 1978; Lackschewitz and Reise 1998; Callaway 2006) the

59   deeper part of those macrobenthos' burrows or tubes. Steady oxygen and/or food supply around the

60   large polychaete burrows or tubes were suggested to be attractive to *U. poseidonis* (see

61   Lackschewitz and Reise 1998; Callaway 2006). How and to what degree such *Urothoe* spp. co-occur

62   with their presumed hosts under sheltered settings remain to be elucidated.

63   In a survey for the density and distribution of macrofauna on an intertidal sandflat in mid-

64   western Kyushu, Japan (Tomioka sandflat; Fig. 1) conducted in the summer of 1979, *Urothoe carda*

65   was the eighth numerically dominant species of a total of 58 species of the benthic community

66   [Tamaki and Kikuchi (1983), with the name, *U. grimaldii*, incorrectly used; total length range:

67   0.8−5.3 mm (A. Tamaki et al., unpubl data)]. The population of *U. carda* occurred mainly in a zone

68   quasi-parallel to the shoreline densely inhabited by the callianassid decapod shrimp (or ghost

69   shrimp), *Nihonotrypaea harmandi* [see Tamaki and Kikuchi 1983, with the name, *Callianassa*

70   *japonica*, incorrectly used (see Manning and Tamaki 1998; Yamada et al. 2017)]. Ghost shrimp are

71   known for their bioturbation effects on sediment and consequent influences on benthic community

72   structure and ecosystem functioning (Pillay and Branch 2011). In the present case, the *N. harmandi*

73   zone occupied the upper one-third part of the sandflat, with shrimp burrows extending over the

74   whole, 10s-cm thick sediment column (above the mollusc shell layer). The accompanying sediment

75   conditions, such as shifting surface sediment and fully oxidized sediment column, were ascribed to

76   dense burrow stands and bioturbation of the shrimp (Tamaki 1984; Tamaki and Suzukawa 1991;

77   Wardiatno et al. 2003). On an estuarine intertidal sandflat in South Africa, the density of a population

78   of *U. grimaldii* in a bed of the ghost shrimp, *Callichirus kraussi*, changed in accordance with the

79   experimental removal and subsequent recovery of the shrimp population (Wynberg and Branch

80   1994). Populations of *U. grimaldii* occurred also on South African open sandy beaches with *C.*

81   *kraussi* absent (Bally 1983). These observations suggest some commensalism of *Urothoe* spp. with

82   ghost shrimp under sheltered settings. Either amphipod residence inside shrimp burrows or its

83   attraction to bioturbated sediment to varying magnitude may be involved in the relationship.

84   One way narrowing down the above possibilities regarding the commensalism is to find

85   amphipods embedded in transparent resin casts of ghost shrimp burrows. Another way is to examine

86   temporal changes in the distributions of the amphipod and ghost shrimp. On the Tomioka sandflat,

87   the sediment surface mixing over the whole shore is caused by seasonal wind-induced waves in the

88   wintertime, while the surface outside the *N. harmandi* zone is stable in the summertime (Tamaki

89   1984, 1987). After 1979, the distribution range of the *N. harmandi* population expanded, having

90   occupied the entire sandflat by 1983 (Tamaki and Suzukawa 1991). This state has continued until

91   2015 (Tamaki and Takeuchi 2016). Both seasonal change around 1979 and some later years'

92   summertime distributions in the *U. carda* population would provide clues to clarifying its

93   dependency on *N. harmandi*. In addition, the amphipod spatial distribution pattern might be different

94   between sexes or between adults and juveniles relative to the ghost shrimp distribution. Finally, since

95   *Urothoe* species are adapted to loosely packed sand (Bousfield 1970), the hardness of sediment may

96   affect the distribution of *U. carda* in relation to that of *N. harmandi* on the present sandflat.

97 Undisturbed state of sediment hardness can be evaluated by vane shear strength *in situ*, where a thin

98 vane blade is inserted into the sediment surface and the sediment maximum resistance to horizontal

99 shearing associated with blade rotation measured (Amos et al. 1988; Sassa and Watabe 2007; Sassa

100 et al. 2011, 2014). The sediment hardness assessed by vane shear strength has been shown to govern

101 the burrowing performances of a crab (Sassa and Watabe 2008), bivalves (Sassa et al. 2011), and

102 amphipods (Sassa et al. 2014) on intertidal sandflats and sandy beaches.

103   The objective of the present study was to show how the dependency of *U. carda* on *N. harmandi*

104 is formed under a sheltered setting of the Tomioka sandflat and to what degree that commensalism

105 is. First, relative to the ghost shrimp distribution and associated sediment conditions including depth

106 of redox potential discontinuity layer and grain-size composition, the following items were

107 examined for the amphipod population: zonation parallel to the shoreline in the summer of 1980;

108 year-round change in the cross-shore distribution during 1980 to 1981; cross-shore distribution in

109 four summers between 1984 and 2015; and cross-shore distributions of adults of both sexes and

110 juveniles in 2015. Second, vertical distribution of amphipods in the sediment column and presence

111 or absence of amphipods inside resin casts of shrimp burrows were checked. Finally, the cross-shore

112 variation in sediment hardness was examined in relation to shrimp and amphipod distributions.

113

114 **Materials and methods**

115 **Monitoring density and distribution of macrofauna and substrate properties**

116   The Tomioka sandflat is located on the northwestern corner of Amakusa-Shimoshima Island

117 (130.037°E; 32°521°N) situated west of Ariake Sound (largest estuary in Kyushu) under a semi-

118 diurnal tidal regime (Fig. 1a). The maximum emersed area of the sandflat during low tide in spring-

119 tide periods spans 3.5 km alongshore and 150−550 m cross-shore in Tomioka Bay, with the

120 maximum tidal range of 3.3 m (Fig. 1b). A rectangular area for the census of macrofauna was

121 established around the northwestern corner of the sandflat, which was 300 m alongshore × 310–325

122 m cross-shore [to the mean low water level in spring-tide periods (MLWS); Fig. 1c]. Although the

123 census area is sheltered to some extent by the northwest- to north-lying headland and sand spit, yet

124 landward transport of some surface-dwelling macrofauna is caused by northerly wind-induced waves

125 during late autumn to early spring (Tamaki 1987; Tamaki and Takeuchi 2016). In the census area,

126 four parallel, cross-shore transects were placed, which were named Transects A, E, G, and J, with the

127 distance between adjacent transects being 60–120 m. On each transect, the stations for sampling

128 were placed every 10 m from the uppermost one at either the sandflat landward edge or 10 m

129 seaward of it to the lowest one at the MLWS; Stn X-Y designates Y m from the landward edge on

130 Transect X. In the first census conducted in July 1979, four faunal assemblage zones quasi-parallel to

131 the shoreline were delineated (Tamaki and Kikuchi 1983). Each zone was named after its dominant

132 or characteristic species (or genus): from upper to lower shore, the spionid polychaete, *Prionospio*

133 *aucklandica* (originally as *P. krusadensis*), *Nihonotrypaea harmandi* (originally as *Callianassa*

134 *japonica*), the bivalve, *Solen strictus*, and the gastropod, *Umbonium moniliferum*. The cross-shore

135 ranges were wider in the *Nihonotrypaea* and *Umbonium* zones than in the other two zones, nearly

136 coincident with those of the habitats of *N. harmandi* and *U. moniliferum*. The whole sediment-

137 column depth spanned 20–30 cm in the *Prionospio* and *Solen* zones, 30–40 cm in the *Nihonotrypaea*

138 zone, and 50–60 cm in the *Umbonium* zone (Tamaki 1984; Takeuchi and Tamaki 2014).

139   Following the above first census' result, Transect G was selected as a representative transect to

140 monitor the subsequent change in the zonation patterns of *Urothoe carda* and *N. harmandi*. The

141 stations visited on each sampling occasion were selected as a subset from the above-mentioned

142 maximum number of stations. The year-round monitoring was conducted during low tide in spring-

143 tide periods from 18 March 1980 to 9 April 1981, most frequently every month. Eighteen to 22

144 stations were visited on each sampling occasion. At each station, first, the thickness of redox

145   potential discontinuity (RPD) layer was measured for a sediment column extracted with a

146   transparent acrylic tube of 100-cm^2 circular cross-sectional area × 35-cm length, in which that layer

147   was identified as the position with clear color changes. Along the boundary circle, the thickness was

148   measured to 1 mm on several points including troughs and crests of small ripples if present (up to

149   1−1.5 cm in crest height) and the mean value calculated [data given in Tamaki (1984)] − briefly, (1)

150   in the *Nihonotrypaea* zone, the entire sediment column was brown, suggesting an oxidized

151   condition; (2) seaward of that zone by up to 40 m (mainly in the *Solen* zone), the surface brown layer

152   was replaced by the gray layer at 10–20-cm depth; and (3) further seaward (in the *Umbonium* zone),

153   the black-colored layer lay immediately below the brown layer at depths < 10 cm. In the present

154   study, the brown layer bottom was defined as the RPD layer depth; in cases that it continued beyond

155   25 cm, the RPD layer thickness was indicated uniformly as 25 cm in the Results. Second, the surface

156   1-cm deep sediment was collected for granulometric analysis by the standard serial sieving protocol

157   (Buchanan and Kain 1971). Three parameters [median φ (Mdφ), sorting coefficient (σ_I: inclusive

158   graphic standard deviation), and mud content (percentage silt-clay fraction in weight)] were

159   obtained. Third, the number of surface openings of *N. harmandi* burrows was counted for four

160   adjacent 25- × 25-cm square plots haphazardly marked on the sandflat surface; one individual of *N.*

161   *harmandi* dwells solitarily in its Y-shaped burrow with two openings (Tamaki and Ueno 1998). At

162   any station in which all burrow-opening diameters were small (1−2-mm φ), as compared with a

163   mixture of both small and large (3−6-mm φ) openings, such a station was recorded as that occupied

164   by only new recruits of the year (Tamaki et al. 1997; Tamaki and Ueno 1998). Finally, at one of the

165   four plots per station, a metal quadrat frame of the same size as above was inserted to a depth of 10

166   cm and the sediment inside excavated, passed through a 0.5-mm mesh sieve, and fixed with 10%

167   neutralized formalin solution for *U. carda* specimens. For the specimens collected in 2015, after

168   their sexes were identified based on the number of articulation in flagellum of antenna 2, the mature

169   and immature categories were determined based on (1) ovigerous or non-ovigerous state (female),

170   (2) presence or absence of calceoli in antenna 2 (male), and (3) total-length-frequency distributions

171   (A. Tamaki et al., unpubl data) and the distributions of the four groups on Transect G examined.

172   On 10–11 August 1980, a census for the whole study area was made along the four transects

173   (Fig. 1c; at 19–22 stations for each), following the same procedure as above.

174   After the complete expansion of the *N. harmandi* population over the sandflat in 1983 (Tamaki

175   and Suzukawa 1991), sampling along Transect G was conducted in each late July–early August of

176   1984, 1997, 2010, and 2015, basically following the same procedure as above, with some

177   modifications. In 1997, 2010, and 2015, the sampling stations had to be altered according to the

178   shortening of the transect length by 20 m due to the reclamation of the uppermost zone of the

179   sandflat in 1991–1993 [see Tamaki and Takeuchi (2016) for details]. The most landward station was

180   re-installed at the landward edge of the intact sandflat, which is named Stn G-0 (2010s). This station

181   is identical to the previous Stn G-20, which is hereafter re-named Stn G-20 (1980s); note that the

182   most landward station in the 1980s was Stn G-10, not Stn G-0. In cases for no misunderstanding

183   about years, the parentheses with years are omitted. The position of the MLWS on the transect has

184   been unchanged, which corresponds to Stn G-310 (1980s) and Stn G-290 (2010s). In 1984 and 1997,

185   the surface burrow-opening count for *N. harmandi* was made at four adjacent unit (25×25-cm^2)

186   plots, while in the 2010s, it was made at eight or nine plots. In 2015, at Stns G-10, 30, and 50, an

187   acrylic tube with cross-sectional area of 100 cm^2 was used for collecting macrofauna, in which a

188   combined sample of six 10-cm deep sediment columns was regarded as equivalent to the usual, one

189   625-cm^2 quadrat sample. Granulometric analysis for the surface 1-cm sediment (3 cm only in 2015)

190   was made by the standard serial sieving protocol for the samples until 1997 and by using a laser

191   diffraction particle-size analyzer (SALD-3100, Shimazu) for those in the 2010s. To estimate the

192   individual numbers of adults and newly-recruited juveniles of *N. harmandi* from the burrow-

193   opening-counts in 2015 from 16 stations (Stns G-0, -10, -30, and every 20-m increment to -290), 10

194   samples of the whole sediment column were extracted with the coring tube at each of Stns G-30, -90,

195   -150, -210, and -270, passed through a 0.5-mm mesh sieve, and fixed on 3 August 2016. In the

196   laboratory, juveniles and adults were separated according to the distinct difference in body size.

197   Based on a yearly stable tendency for the juvenile distribution pattern over the transect (Tamaki et al.

198   1997), the juvenile-to-adult number ratio was applied to the 2015 data, in which the two adjacent

199   stations about each of the above five stations with core samples were assumed to take the same ratio

200   (the ratio at Stn G-30 was applied also to Stn G-0).

201   During ± 1 h around the lowest-tide time on 1 August 2015, the surface elevation along Transect

202   G was measured to 1 mm with TRIMBLE R4 GNSS System (Trimble). At each of Stns G-0 to -290

203   (16 stns), the level of the groundwater table was measured to 1 mm with a ruler 1 min after

204   shoveling the surface sediment. Then, sediment hardness for the sub-surface depths of 10 mm and 40

205   mm were measured with a vane blade of 40-mm φ and 10-mm depth (FTD2CN-S, Seiken) and of

206   20-mm φ and 40-mm depth (FTD5CN-S, Seiken), respectively, at a point randomly placed between

207   surface burrow openings of *N. harmandi*. To compare the sediment hardness values at 10-mm depth

208   among the sediments containing a small burrow opening with 1–2-mm φ, a large one with 4–6-mm

209   φ, and outside burrow openings, measurements were made with FTD2CN-S at a location with high

210   shrimp densities around the lowest-tide time on 1 August 2016 ($n = 6$ for each burrow-opening size

211   and $n = 13$ for the latter). In the measurement for the former two, the center of the vane blade was

212   positioned exactly at each burrow opening. In both 2015 and 2016, the weather was fine and calm.

213

214   **Vertical distribution of *U. carda* in the sediment column**

215   To determine the vertical distribution of *U. carda* individuals in the substrate inhabited by *N.*

216   *harmandi* on the Tomioka sandflat during low tide, sediment columns were extracted with a

217   graduated acrylic tube, and sectioned into multiple layers, passed through a 0.5-mm mesh sieve, and

218   fixed with 10% neutralized formalin solution. On 15 August 1981, each of the three sediment

219   columns of a cross-sectional area of 100 cm^2 to a 23-cm depth (brown in color) at Stn G-20 were

220   sectioned into six layers of 0 (= surface)–1, 1–2, 2–3, 3–5, 5–10, and 10–23 cm and the samples for

221   each layer combined. On 13 May 2017, each of the six sediment columns of a cross-sectional area of

222   24 cm^2 to a 15-cm depth (brown in color) at Stn G-30 were sectioned into three layers of 0–5, 5–10,

223   and 10–15 cm and the samples for each layer combined.

224

225   **Casting burrows of *N. harmandi***

226   To examine whether or not individuals of *U. carda* dwell inside *N. harmandi* burrows, polyester

227   resin casts of aggregated burrows were made over a circular area enclosed with a 23.5-cm φ bottom-

228   removed polypropylene container around Stn G-10 on the Tomioka sandflat during low tides from

229   27 to 28 May 2017, following the burrow casting protocol given in Tamaki and Ueno (1998). In the

230   laboratory, amphipods embedded in the transparent burrow casts were searched for.

231

232   **Results**

233   **Vertical distribution of *Urothoe carda* in the sediment column**

234   In August 1981, all 191 individuals of *Urothoe carda* in the 23-cm deep sediment column on the

235   Tomioka sandflat were found from the upper 5-cm layer, with 14% in 0–1 cm, 56.5% in 1–2 cm,

236   23.5% in 2–3 cm, and 6% in 3–5 cm. In May 2017, 112 of a total of 113 individuals present in the

237   15-cm deep sediment column were found from the upper 5-cm layer, with 1 individual in 5–10 cm.

238

239   **Burrow casts of *Nihonotrypaea harmandi***

240   In the 434-cm^2 enclosed area of the Tomioka sandflat in May 2017, the number of casts of Y-

241   shaped burrows of *Nihonotrypaea harmandi* was 34, including those with either one of the two

242   segments above the node of the *Y* incomplete (Fig. 2). The maximum depth of each burrow ranged

243   from 9.0 to 27.1 cm, with mean (± SD) being 18.2 (± 5.8) cm. The depth of the node of the *Y* ranged

244   from 6.7 to 16.9 cm, with mean (± SD) being 11.6 (± 2.4) cm. The number of casts with only a

245   single shaft retrieved was 19. No individuals of *U. carda* were embedded in the burrow casts, with

246   341 expected individuals residing in the surface 5-cm layer of the enclosed area, based on their

247   nearby density (113 inds 144 cm^{-2}: preceding sub-section).

248

249   **Temporal change in the transect distributions of *N. harmandi* and *U. carda* during 1980−1981**

250   Over the four transects on the Tomioka sandflat on 10−11 August 1980, *N. harmandi* burrows

251   and *U. carda* individuals showed a common zonation pattern quasi-parallel to the shoreline (Fig. 3).

252   The main zone occupied by *N. harmandi* burrows, with RPD depths ≥ 25 cm, shifted from the upper

253   half of Transect J to the upper one-third of Transect A. The overall mean (± SD) *N. harmandi* density

254   from mean density at every station with a non-zero value (including the stations with RPD depths <

255   25 cm), as estimated from burrow-opening counts, was 182 (± 138) shrimps m^{-2} [n = 35 (stns)].

256   Almost all individuals of *U. carda* occurred in the main *N. harmandi* zone, with mean density over

257   the four transects being 43.8 inds 625 cm^{-2} (n = 77). On each transect, two separate density-peaks

258   were present in the upper and mid- to lower part of the *Nihonotrypaea* zone, respectively. On

259   Transects G, E, and A, a substantial part of each transect population of *U. carda* occurred also 10−20

260   m seaward of the seaward limit of the *N. harmandi* zone (i.e. in the *Solen* zone), with RPD depths of

261   10−17 cm. Beyond the *Solen* zone [i.e. in the *Umbonium* zone (to the MLWS)], the RPD depths lay

262   closer to the surface, with mean (± SD) for the four transects being 3.4 (± 1.2) cm (n = 30).

263   Along Transect G during March 1980 to April 1981, the seaward limit of the *N. harmandi* adult-

264   inhabited zone expanded by 20 m, from Stn G-130 to Stn G-150, in October, when Stn G-260 was

265   also established as a separate zone in the lower shore (gray columns in Fig. 4a–m). This colonization

266   was caused by both adult immigration and settlement of new recruits (Tamaki and Ingole 1993;

267   Tamaki 1994). The overall mean density through the year estimated from the mean burrow-opening

268   density at every station with a non-zero value was 181 shrimps m^{-2} ($n = 170$). The mean density of

269   *U. carda* on each sampling occasion ranged from 57.9 (May 1980) to 102.0 (April 1980) inds 625

270   cm^{-2}, with overall mean ($\pm$ SD) through the year being 81.7 ($\pm$ 13.1) inds 625 cm^{-2} ($n = 13$). The

271   population of *U. carda* showed a clear seasonal distribution pattern relative to the *Nihonotrypaea*

272   zone. During July to September, most of the population was confined to the *Nihonotrypaea* zone,

273   and a substantial part was extended beyond that zone to the lowest shore during December to May,

274   with the distributions in June and October transitional. The extended and contracted phases of the *U.*

275   *carda* population in the *Umbonium* zone (Stns G-180–310) were in parallel with the seasonally

276   changing RPD depths, of which mean ($\pm$ SD) values were 6.8 ($\pm$ 2.4) cm ($n = 21$) during March to

277   May 1980, 5.0 ($\pm$ 2.7) cm ($n = 7$) in June, 2.6 ($\pm$ 1.0) cm ($n = 38$) during July to September, 5.1 ($\pm$

278   2.1) cm ($n = 6$; excluding Stn G-260) in October, and 6.2 ($\pm$ 1.5) cm ($n = 18$; excluding Stn G-260)

279   during December 1980 to April 1981. During June to October, there were largely two separate

280   density-peaks of *U. carda* in the upper and mid- to lower *Nihonotrypaea* zone, respectively, and a

281   substantial part of the transect population occurred 10–30 m seaward of the seaward limit of the *N.*

282   *harmandi* adult-inhabited zone (i.e. in the *Solen* zone), with RPD depths of 8–16 cm. At Stn G-260

283   in October, both *N. harmandi* density (mean of 240 shrimps m^{-2}) and RPD depth (12 cm) were

284   greater than those values at the other lower-shore stations. The *U. carda* density was higher at Stn G-

285   260 than at the two adjacent stations.

286

287   **Temporal change in the transect distributions of *N. harmandi* and *U. carda* during 1984–2015**

288   Along Transect G on the Tomioka sandflat in 1984, 1997, 2010, and 2015, all stations were

289   occupied by *N. harmandi*, with mean (±SD) shrimp densities over the stations (inds m^{-2}), as

290   estimated from burrow-opening counts, declining from 461 (± 104) in 1984 [n = 16 (stns); Stn G-10

291   (uppermost station: *Prionospio* zone) excluded], via 214 (± 63) in 1997 (n = 15; Stn G-0 excluded),

292   to 69 (± 38) in 2010 (n = 18) and 104 (± 38) in 2015 (n = 16) (Fig. 5a–d). The marked reduction in

293   shrimp densities from 1984 to 1997 was caused by heavy predation by the stingray, *Dasyatis akajei*,

294   which continued from 1995 onward (up to the present) (Takeuchi and Tamaki 2014; Tamaki and

295   Takeuchi 2016). Stingrays excavate deep pits during foraging for shrimps, which had the maximum

296   impact on the shrimp population in the mid-shore due to the thinnest sediment columns there (20s

297   cm; Takeuchi and Tamaki 2014). Also in 2010, the spatially different stingray impact was reflected

298   in the higher shrimp densities in the upper and lower shores and the lowest ones in the mid-shore. In

299   2015, the densities in the mid-shore were not lower than in the upper and lower shores. This was

300   most probably due to the higher new recruits' densities in the mid- to lower shore, as indicated in the

301   distribution of estimated densities of juveniles and adults over the transect (Fig. 5e).

302   In 1984, 1997, and 2015, the RPD depths were > 25 cm at all stations except for Stn G-10 (data

303   not shown in Fig. 5). In 2010, although most RPD depths were > 25 cm, the values of 8–20 cm

304   emerged in the mid-shore (Fig. 5c).

305   In 1984, *Urothoe carda* occurred over the whole transect, with 26–147 (range) and 74.2 [mean; n

306   = 17 (stns)] inds 625 cm^{-2} (Fig. 5a; hereafter 625 cm^{-2} is omitted for density values). In 1997, the

307   densities over the whole transect were lower than in 1984, with up to 65 inds and the mean of 9.3

308   inds (n = 16), and 75% of the whole members occurred from the upper 50-m part of the transect

309   (Fig. 5b). In 2010, the same tendency as in the ghost shrimp distribution was observed, with the

310   highest *U. carda* densities of 51 and 105 inds being at Stns G-30 and G-220, respectively, and the

311   mean density over the whole transect being 34.6 inds (n = 18) (Fig. 5c). Also in 2015, the lower

312   densities in the mid-shore was sandwiched by the highest densities in the upper and lower shores

313   (107–108 and 125 inds at Stns G-30–G-50 and G-270, respectively), with the mean density over the

314   whole transect being 64.4 inds ($n = 16$) (Fig. 5d). The spatial variation in the density of *U. carda*

315   resembled that of *N. harmandi* adults (Fig. 5e). Furthermore for *U. carda*, in the upper-half shore,

316   the mature and immature individuals of both sexes were distributed separately in its lower and upper

317   parts, while in the lower-half shore, the distribution centers of mature and immature individuals of

318   both sexes were at the two lowest stations, decreasing toward each lowest density at Stn G-130,

319   though the tendency in the mature male was less clear due to its low densities (Fig. 5f).

320

321   **Temporal change in sediment grain-size composition and snapshot underground properties**

322   The distributions of Mdφ, σ_I, and mud content of the surface sediment along Transect G on the

323   Tomioka sandflat in July–August of 1980–2015 are shown in Fig. 6a–c, respectively. In all years,

324   the particle was finer landward, as is general for tidal flats. In 1980 and 1984, from lowest to

325   uppermost shores, the sediment type shifted from well-sorted to moderately-sorted, fine to coarser

326   very fine sand. The mud content in 1980 exhibited a dip in the lower part of the *Nihonotrypaea* zone

327   (Stns G-20–G-130). In 1997, as compared with the 1980s, especially in the transect mid- to lowest

328   part, (1) median particle diameter became slightly larger within the fine sand category, (2) sorting

329   became largely better within the moderately well-sorted category, and (3) mud content became less.

330   This trend continued afterward, especially with a marked increase in median grain size and decrease

331   in mud content. In 2010 and 2015, from lowest to uppermost shore, basically, the values of Mdφ

332   shifted from medium to coarser-fine sand categories, and the values of σ_I shifted from very well- to

333   moderately-sorted categories. The greater spatial variations in the Mdφ and σ_I in 2015 than in 2010

334   might be due to the deeper sediment samples in the former with greater heterogeneities (3 vs. 1 cm).

335   The locally high mud contents at Stns G-150 and -190 in 2010 corresponded to the lowest densities

336   of *N. harmandi* there (Fig. 5c).

14

337   The sandflat surface elevation inclined gently along Transect G in 2015, with a gradient of ca.

338   1/250 over 290 m. The groundwater tables were close to the sandflat surface [range = −2.5 (below

339   surface) to 2.5 (above surface: overflow) cm; mean (± SD) = 0.6 (± 1.4) cm; n = 16 (stns)]. The

340   distribution of sediment hardness over the transect is shown in Fig. 7. The vane shear strengths at 4-

341   cm depth were higher in the upper and lower shores and lowest in the mid-shore, coincident with the

342   spatial variation in the densities of both *U. carda* individuals (Fig. 5d, f) and *N. harmandi* adults

343   (Fig. 5e), while those strengths at 1-cm depth varied in a small range around a much lower value.

344   In comparing the values of sediment hardness among the points at small and large burrow

345   openings of *N. harmandi*, and at outside-burrow-opening points in 2016, the value for sediments on

346   another intertidal sandflat [Okoshiki sandflat in Ariake Sound (cf. Yamada and Kobayashi 2007);

347   Fig. 1a] during low tide in 2010 were used additionally (n = 5; S. Sassa and S. Yang, unpubl data)

348   (Fig. 8). That sandflat is dominated by large sand waves and shares essentially the same sediment

349   granulometric characteristics (median diameters: 0.18–0.28 mm) and the groundwater table up to the

350   surface (in troughs of the sand waves) with those of the Tomioka sandflat. Although a large number

351   of *N. harmandi* and *N. japonica* existed in 1998 (Wardiatno et al. 2003), no surface burrow openings

352   of both species were found at the time of measurement in 2010 (points with "no burrow openings").

353   The lowered abundance of *N. japonica* population in recent years are common to several intertidal

354   sandflats in Ariake Sound (Takeuchi et al. 2013). The difference in the median values of vane shear

355   strength among the four points was tested for significance by Kruskal-Wallis test, followed by Steel-

356   Dwass multiple comparison test, using "R"-based software "EZR" (Kanda 2013). There was a

357   significant difference among the four points (Kruskal-Wallis X^2 = 25.7, df = 3, P < 0.001), and the

358   mean-value order from high to low was: large burrow opening, small burrow opening, no burrow

359   openings, and outside-burrow openings. Except for the pair between small and no burrow openings,

360   all other pairs were significantly different (P < 0.01 or 0.05).

361

Discussion

The stable association of *Urothoe carda* with *Nihonotrypaea harmandi* on the Tomioka sandflat
was evident from (1) their common upper-shore distribution on the four transects in the summer of
1980 (Fig. 3) and on one of these transects (Transect G) in the summertime of 1980 (Fig. 4e–i) and
(2) their whole-shore distributions on Transect G in the summers of 1984, 2010, and 2015, when the
entire sandflat had been occupied by *N. harmandi* (Fig. 5a, c, d). Through these years, the mean
density of *U. carda* (no. inds 625 cm^{-2}) over Transect G varied in a small range from 35 to 82. The
mean density value was 9 in 1997, when most individuals were in the upper part of the transect
despite the whole-shore distribution of *N. harmandi* (Fig. 5b). It is thus inferred that the base of the
U. carda population lay primarily in the upper *N. harmandi* zone and that, in its higher-abundance
phase, *excess* individuals of the *U. carda* population made a range extension into the mid- to lower
N. harmandi zone. Frequent shuffling their dwelling sites on the present sandflat during nocturnal
submergence periods is suggested (A. Tamaki et al., unpubl data). In 2010 and 2015, the *U. carda*
densities peaked in the upper and lower shores separately, with the lowest densities in the mid-shore
(Fig. 5c, d). This was in parallel with the spatial variation in the *N. harmandi* density, especially that
of adults, not of juveniles (Fig. 5e, f). In the upper-half shore in 2015, the center of the distributions
of mature individuals (adults) of both sexes of *U. carda* was at 90 m from the uppermost shoreline,
while that of immature individuals (juveniles) was within 50 m from there (Fig. 5f). Such a bimodal
distribution within the upper shore was observed on most sampling occasions during 1980 to 1981
(Figs. 3 and 4), which might have also been due to the segregation of adults and juveniles. The peak
position of juveniles situated landward of that of adults was recorded for a number of macrobenthic
species on the present sandflat, which was suggested to be caused by hydrodynamic sorting by body
size (Tamaki 1987; Tamaki and Suzukawa 1997; Tamaki and Takeuchi 2016). The salinity of the

385   groundwater along Transect G measured during low tide in June, 1998 indicated the values of

386   9.0–17.4 in the upper 50-m zone and 31.2–32.0 in the seaward zone, suggesting the penetration of

387   ground freshwater from the land into the former zone (Wardiatno et al. 2003). The low salinity in the

388   upper sandflat may be sub-optimum for *U. carda* adults but optimum for some species including

389   *Prionospio aucklandica* and the anthurid isopod, *Cyathura muromiensis* (see Tamaki and Kikuchi

390   1983). On some intertidal sandflats, a peculiar benthic assemblage occurred in each uppermost area

391   with ground freshwater discharge (Zipperle and Reise 2005; Dale and Miller 2008).

392   Despite its long-term stability, the association between *U. carda* and *N. harmandi* on the

393   Tomioka sandflat was not always obligate. This was evident from the observations on the extended

394   distribution of *U. carda* beyond the *N. harmandi*-inhabited zone by 10–30 m seaward along the four

395   transects and Transect G in the summer of 1980 (Figs. 3 and 4d–g) and by all remaining length of

396   Transect G during winter to spring in 1980 and 1981 (Fig. 4a–c, k–m). Thus, *U. carda* can be

397   regarded as a facultative commensal of *N. harmandi*. As no individuals of *U. carda* were found

398   inside the resin casts of *N. harmandi* burrows (Fig. 2), they are assumed to exist in the interstitial

399   space between these burrows. Such a micro-scale distribution pattern is similar to that of *U.*

400   *poseidonis* associated with, but not inside, the tubes of the terebellid polychaete, *Lanice conchilega*,

401   on an intertidal sandflat (Callaway 2006). The dwelling depth in the sediment column was 0–5 cm

402   for *U. carda* and down to 10–15 cm for *U. poseidonis* (see Lackschewitz and Reise 1998; Callaway

403   2006). A similar association between free-burrowing amphipod and ghost shrimp may exist for *U.*

404   *grimaldii* and *Callichirus kraussi* on South African estuarine intertidal sandflats (cf. Wynberg and

405   Branch 1994). Facultative commensalism of smaller macrobenthos with *N. harmandi* on the present

406   sandflat was reported for the cirolanid isopod, *Eurydice nipponica*, which primarily occurs on

407   exposed sandy beaches along the coastline of Kyushu (Tamaki and Suzukawa 1991, 1997). Some

408   bioturbation effects of *N. harmandi* would become beneficial to both *U. carda* and *E. nipponica*

409   under the present sheltered setting. Compared with *U. carda*, *E. nipponica* was confined to the

410   *Nihonotrypaea* zone year-round in 1980–1981, and not only distribution range but also population

411   size increased from 1984 onward (Tamaki and Suzukawa 1991, 1997; A. Tamaki, unpubl data).

412   Though either facultative or obligate one is unknown, callianassids-associated commensalism in

413   highly mobile smaller macrobenthos on sandy bottoms was reported for ostracods (Riddle 1988),

414   amphipods (Posey 1986; Riddle 1988), bivalves (Aller and Dodge 1974; Tudhope and Scoffin 1984),

415   and polychaetes (Riddle 1988; Wynberg and Branch 1994).

416   For *U. poseidonis* individuals associated with their presumed polychaete hosts, the sub-surface

417   permeable sediment around those burrows or tubes was suggested to form an attractive interstitial

418   space with elevated dissolved oxygen concentration and/or increased food supply (Lackschewitz and

419   Reise 1998; Callaway 2006). Increased permeability in the sediment may also enable the amphipod

420   to filter-feed more efficiently there (cf. Bousfield 1970). The thickness of the surface oxidized layer

421   in yellow or brown color above the RPD depth, with the reduced layer beneath it in gray to black

422   colors, nearly coincides with the thickness of the surface oxygenated layer on sheltered intertidal

423   sandflats and dissipative sandy beaches (Fenchel and Riedl 1970; McLachlan 1978; McLachlan and

424   Turner 1994). Thus, although pore-water dissolved oxygen concentration of the sediment was not

425   measured in the present study, the surface oxidized sediment layer thickness (SOSLT) could be used

426   as a proxy for the surface oxygenated sediment layer thickness. Consistently through 1980 to 2015,

427   the whole sediment column in the zone densely inhabited by *N. harmandi* adults was oxidized,

428   where the population of *U. carda* mainly occurred (Figs. 3–5). The oxidized substrate also affects

429   the bacterial community on the present sandflat (Wada et al. 2016). The surface sediment's greater

430   median size, better sorting, and lower content of silt-clay that took place through these years (Fig.

431   6a–c) could also make the sediment more permeable. These granulometric parameter changes might

432   have been caused by the bioturbation of *N. harmandi*, horizontally expelling finer fractions of the

433   surface sediment away and burying its very coarser fraction deep into the sediment column (Tamaki

434   1994; Wardiatno et al. 2003), of which mechanism remains to be examined. The range of those

435   sediment grain-size parameter values through all years appears acceptable by *U. carda*. In the zone

436   seaward of the *N. harmandi*-inhabited upper shore during 1980 to 1981, the SOSLT and the

437   intermediate to high densities of *U. carda* occurred coincidently: (1) the extended distributions of

438   both oxidized sediment column and *U. carda* by 10–30 m seaward (into the *Solen* zone) in the

439   summertime, (2) the smallest SOSLT and the absence or quite low densities of *U. carda* beyond the

440   *Solen* zone in the summertime, with dense spionid polychaete tube mats in the *Solen* to upper

441   *Umbonium* zone (Tamaki and Kikuchi 1983; Tamaki 1984, 1985), and (3) the larger SOSLT and the

442   intermediate or high densities of *U. carda* in the *Solen* to *Umbonium* zones through the winter and

443   early spring. The threshold SOSLT allowing the existence of *U. carda* appeared to be 5 cm (Figs. 3

444   and 4), which was equal to the maximum depth of *U. carda* individuals in the sediment column.

445   Regarding a possible mechanism causing the above event (1), it is noteworthy that the hydraulic

446   activity of the ghost shrimp, *Neotrypaea californiensis*, induced lateral transport of oxygenated water

447   into the surrounding sediment as well as into their burrows in laboratory aquaria (Volkenborn et al.

448   2012). Woodin et al. (2010) proposed that those large bioturbators residing in burrows with

449   permeable walls, including arenicolid polychaetes, be called infaunal hydraulic ecosystem engineers.

450   The seasonal change in the SOSLT in the above events (2) and (3) was in accordance with that of the

451   sediment silt-clay content at Stn G-160 (1980s), ranging from 0.7% in winter to 1.7% in summer,

452   and with the greater degree of the sediment surface mixing by northerly wind-induced waves during

453   the late autumn to early spring (Tamaki 1984, 1987). Such a seasonal change is generally found for

454   sheltered intertidal sandflats, with the deposition of oxygen-consuming organic matter during the

455   warmer and calmer season and the wind-wave disturbance during the colder and stormier season

456   (Fenchel and Riedl 1970; McLachlan 1978).

457   The lateral and vertical sediment displacement by the *N. harmandi* population in high densities

458   on the Tomioka sandflat may soften its inter-burrow substrate for *U. carda* individuals to efficiently

459   move through and re-burrow into. The sediment hardness of intertidal sandflats depends on suction

460   (i.e. negative pore water pressure relative to atmospheric pressure) and their packing states, the latter

461   changing considerably with suction dynamics under tide-induced groundwater table fluctuations

462   (Sassa and Watabe 2007). On sandy beaches, the sediment hardness due to suction development and

463   suction-dynamics-induced sediment compaction acted as a limiting factor for the survival and

464   distributions of amphipods (*Talorchestia brito* and *Haustorioides japonicus*) by preventing their

465   burrowing behavior (Sassa et al. 2014). On the Tomioka sandflat, the groundwater table was nearly

466   the same as the surface elevation during low tides, indicating that suction is absent throughout tidal

467   cycles and that the hardness of the sediment depends solely on its packing state. The shape of the

468   outline of vane shear strengths at 4-cm depth over Transect G (Fig. 7) was very similar to that for

469   adult *N. harmandi* density (Fig. 5e) [and for *U. carda* density (Fig. 5f)]. This would have reflected a

470   work for rotating the vane blade to destroy burrows encountered at that depth (Fig. 2), which was

471   confirmed by the highest shear strength value at 1-cm depth exactly beneath the large burrow

472   openings and the second highest value exactly beneath the small burrow openings recorded in 2016

473   (Fig. 8). The 1-cm depth shear strengths in 2015 comparable to those outside and lower than at

474   burrows in 2016 would represent the packing state of the sediment outside *N. harmandi* burrows.

475   Such outside-burrow-opening shear strength on the Tomioka sandflat was significantly lower than

476   the shear strength with no burrows on the Okoshiki sandflat (Fig. 8), despite the same sediment-Mdφ

477   ranges between the two sandflats and no suctions during low tides in trough parts of sand waves on

478   the latter sandflat (Yamada and Kobayashi 2007; Sassa and Watabe 2009). This suggests that the

479   bioturbating activity of *N. harmandi* individuals altered the sediment packing state through the

480   displacement and rearrangement of sand particles among their highly dense burrows, which resulted

20

481   in the looser and more permeable sediments than those solely subjected to physical displacement.

482   In conclusion, for some species of *Urothoe* on sheltered intertidal sandflats, the bioturbation or

483   tube/burrow of some large macrobenthos would provide amphipods with more permeable and softer

484   sediments, generating elevated dissolved oxygen concentration and increased pore space to possibly

485   facilitate amphipods' efficient burrowing and filter-feeding. Facultative commensalism of highly

486   mobile species with those sedentary large macrofauna would form one stable functional component

487   of the benthic community among other components on sheltered sandflats, including the one due to

488   amensalism exerted from ghost shrimps on filter-feeding molluscs (e.g. Tamaki and Takeuchi 2016).

489

504

505   **References**

506   Aller RC, Dodge RE (1974) Animal−sediment relations in a tropical lagoon Discovery Bay, Jamaica.

507   J Mar Res 32:209−232

508   Amos CL, Van Wagoner NA, Daborn GR (1988) The influence of subaerial exposure on the bulk

509   properties of fine-grained intertidal sediment from Minas Basin, Bay of Fundy. Estuar Coast

510   Shelf Sci 27(1):1−13. doi: 10.1016/0272-7714(88)90028-5

511   Bally R (1983) Intertidal zonation on sandy beaches of the west coast of South Africa. Cahiers de

512   Biologie Marine 24:85−103

513   Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda

514   (except marine Gammaroidea). Part 2. Records of the Australian Museum Supplement

515   13(2):419−866. doi: 10.3853/j.0812-7387.13.1991.367

516   Bousfield EL (1970) Adaptive radiation in sand-burrowing amphipod crustaceans. Chesapeake Sci

517   11(3):143−154. doi: 10.2307/1351237

518   Buchanan JB, Kain JM (1971) Measurement of the physical and chemical environments. In: Holme

519   NA, McIntyre AD (eds) Methods for the Study of Marine Benthos. Blackwell, Oxford, pp 30−58

520   Callaway R (2006) Tube worms promote community change. Mar Ecol Prog Ser 308:49−60. doi:

521   10.3354/meps308049

522   Dale RK, Miller DC (2008) Hydrologic interactions of infaunal polychaetes and intertidal

523   groundwater discharge. Mar Ecol Prog Ser 363:205−215. doi: 10.3354/meps07455

524   Fenchel TM, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized

525   layer of marine sand bottoms. Mar Biol 7(3):255−268. doi: 10.1007/BF00367496

526   Fernandez-Gonzalez V, Fernandez-Jover D, Toledo-Guedes K, Valero-Rodriguez JM, Sanchez-Jerez

527   P (2014) Nocturnal planktonic assemblages of amphipods vary due to the presence of coastal

528   aquaculture cages. Mar Environ Res 101:22−28. doi: 10.1016/j.marenvres.2014.08.001

529   Fincham AA (1970) Amphipods in the surf plankton. J Mar Biol Assoc UK 50(1):177–198. doi:

530   10.1017/S0025315400000709

531   Kanda Y (2013) Investigation of the freely available easy-to-use software 'EZR' for medical

532   statistics. Bone Marrow Transplant 48:452–458. doi: 10.1038/bmt.2012.244

533   Lackschewitz D, Reise K (1998) Macrofauna on flood delta shoals in the Wadden Sea with an

534   underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe*

535   *poseidonis*. Helgoländer Meeresunters 52(2):147–158. doi: 10.1007/BF02908744

536   Manning RB, Tamaki A (1998) A new genus of ghost shrimp from Japan (Crustacea: Decapoda:

537   Callianassidae). Proc Biol Soc Wash 111(4):889–892

538   McLachlan A (1978) A quantitative analysis of the meiofauna and the chemistry of the redox

539   potential discontinuity zone in a sheltered sandy beach. Estuar Coast Shelf Sci 7(3):275–290. doi:

540   10.1016/0302-3524(78)90110-X

541   McLachlan A, Turner I (1994) The interstitial environment of sandy beaches. PSZN I: Mar Ecol

542   15(3–4):177–211. doi: 10.1111/j.1439-0485.1994.tb00053.x

543   Pillay D, Branch GM (2011) Bioengineering effects of burrowing thalassinidean shrimps on marine

544   soft-bottom ecosystems. Oceanogr Mar Biol Annu Rev 49:137–192

545   Posey MH (1986) Changes in a benthic community associated with dense beds of a burrowing

546   deposit feeder, *Callianassa californiensis*. Mar Ecol Prog Ser 31:15–22

547   R Core Team (2015) R: a language and environment for statistical computing. R Foundation for

548   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed 11 Oct 2017

549   Riddle MJ (1988) Cyclone and bioturbation effects on sediments from coral reef lagoons. Estuar

550   Coast Shelf Sci 27:687–695. doi: 10.1016/0272-7714(88)90075-3

551   Sassa S, Watabe Y (2007) Role of suction dynamics in evolution of intertidal sandy flats: field

552   evidence, experiments, and theoretical model. J Geophys Res 112:F01003. doi:

553   10.1029/2006JF000575

554   Sassa S, Watabe Y (2008) Threshold, optimum and critical geoenvironmental conditions for

555   burrowing activity of sand bubbler crab, *Scopimera globosa*. Mar Ecol Prog Ser 354:191−199.

556   doi: 10.3354/meps07236

557   Sassa S, Watabe Y (2009) Persistent sand bars explained by geodynamic effects. Geophys Res Lett

558   36:L01404. doi:10.1029/2008GL036230

559   Sassa S, Watabe Y, Yang S, Kuwae T (2011) Burrowing criteria and burrowing mode adjustment in

560   bivalves to varying geoenvironmental conditions in intertidal flats and beaches. PLoS ONE

561   6(9):e25041. doi: 10.1371/journal.pone.0025041

562   Sassa S, Yang S, Watabe Y, Kajihara N, Takada Y (2014) Role of suction in sandy beach habitats and

563   the distributions of three amphipod and isopod species. J Sea Res 85:336−342. doi:

564   10.1016/j.seares.2013.06.005

565   Sudo H (1988) Diurnal rhythms in predatory fish and amphipod prey. In: Hanyu I, Tabata M (eds)

566   Daily Rhythmic Activities in Aquatic Animals. Kouseisha-Kouseikaku, Tokyo, pp 117−183 (in

567   Japanese)

568   Takeuchi S, Tamaki A (2014) Assessment of benthic disturbance associated with stingray foraging

569   for ghost shrimp by aerial survey over an intertidal sandflat. Cont Shelf Res 84:139−157. doi:

570   10.1016/j.csr.2014.05.007

571   Takeuchi S, Takahara Y, Agata Y, Nasuda J, Yamada F, Tamaki A (2013) Response of suspension-

572   feeding clams to natural removal of bioturbating shrimp on a large estuarine intertidal sandflat in

573   western Kyushu, Japan. J Exp Mar Biol Ecol 448:308−320. doi: 10.1016/j.jembe.2013.07.018

574   Tamaki A (1984) Structural characteristics of an intertidal sand flat in Tomioka Bay, Amakusa, west

575   Kyushu. Publ Amakusa Mar Biol Lab Kyushu Univ 7:125−150

576   Tamaki A (1985) Inhibition of larval recruitment of *Armandia* sp. (Polychaeta: Opheliidae) by

577   established adults of *Pseudopolydora paucibranchiata* (Okuda) (Polychaeta: Spionidae) on an

578   intertidal sand flat. J Exp Mar Biol Ecol 87(1):67−82. doi: 10.1016/0022-0981(85)90193-5

579   Tamaki A (1987) Comparison of resistivity to transport by wave action in several polychaete species

580   on an intertidal sand flat. Mar Ecol Prog Ser 37:181−189

581   Tamaki A (1994) Extinction of the trochid gastropod, *Umbonium* (*Suchium*) *moniliferum* (Lamarck),

582   and associated species on an intertidal sandflat. Res Popul Ecol 36(2):225−236. doi:

583   10.1007/BF02514939

584   Tamaki A, Ingole B (1993) Distribution of juvenile and adult ghost shrimps, *Callianassa japonica*

585   Ortmann (Thalassinidea), on an intertidal sandflat: intraspecific facilitation as a possible pattern-

586   generating factor. J Crustac Biol 13(1):175−183. doi: 10.1163/193724093X00543

587   Tamaki A, Kikuchi T (1983) Spatial arrangement of macrobenthic assemblages on an intertidal sand

588   flat, Tomioka Bay, west Kyushu. Publ Amakusa Mar Biol Lab Kyushu Univ 7:41−60

589   Tamaki A, Suzukawa K (1991) Co-occurrence of the cirolanid isopod *Eurydice nipponica* Bruce &

590   Jones and the ghost shrimp *Callianassa japonica* Ortmann on an intertidal sand flat. Ecol Res

591   6:87−100. doi: 10.1007/BF02353872

592   Tamaki A, Suzukawa K (1997) Life history and zonation dynamics of the cirolanid isopod, *Eurydice*

593   *nipponica* Bruce & Jones, on an intertidal sandflat in western Kyushu, Japan. Crustac Res

594   26:83−102. doi: 10.18353/crustacea.26.0_83

595   Tamaki A, Takeuchi S (2016) Persistence, extinction, and recolonization of an epibenthic gastropod

596   population on an intertidal sandflat: 35-y contingent history of a key species of the benthic

597   community in metapopulation and metacommunity contexts. J Shellfish Res 35(4):921−967. doi:

598   10.2983/035.035.0419

599   Tamaki A, Ueno H (1998) Burrow morphology of two callianassid shrimps, *Callianassa japonica*

600   Ortmann, 1891 and *Callianassa* sp. (= *C. japonica*: de Man, 1928) (Decapoda: Thalassinidea).

601   Crustac Res 27:28–39. doi: 10.18353/crustacea.27.0_28

602   Tamaki A, Ingole B, Ikebe K, Muramatsu K, Taka M, Tanaka M (1997) Life history of the ghost

603   shrimp, *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in

604   western Kyushu, Japan. J Exp Mar Biol Ecol 210(2):223–250. doi: 10.1016/S0022-

605   0981(96)02709-8

606   Tudhope AW, Scoffin TP (1984) The effects of *Callianassa* bioturbation on the preservation of

607   carbonate grains in Davies Reef lagoon, Great Barrier Reef, Australia. J Sediment Petrol

608   54:1091–1096

609   Vader W (1978) Associations between amphipods and echinoderms. Astarte 11:123–134

610   Volkenborn N, Polerecky L, Wethey DS, DeWitt TH, Woodin SA (2012) Hydraulic activities by

611   ghost shrimp *Neotrypaea californiensis* induce oxic-anoxic oscillations in sediments. Mar Ecol

612   Prog Ser 455:141–156. doi: 10.3354/meps09645

613   Wada M, Urakawa T, Tamaki A (2016) Dynamics of bacterial community structure on intertidal

614   sandflat inhabited by the ghost shrimp *Nihonotrypaea harmandi* (Decapoda: Axiidea:

615   Callianassidae) in Tomioka Bay, Amakusa, Japan. Gene 576(2):657–666. doi:

616   10.1016/j.gene.2015.10.017

617   Wardiatno Y, Shimoda K, Koyama K, Tamaki A (2003) Zonation of congeneric callianassid shrimps,

618   *Nihonotrypaea harmandi* (Bouvier, 1901) and *N. japonica* (Ortmann, 1891) (Decapoda:

619   Thalassinidea), on intertidal sandflats in the Ariake-Sound estuarine system, Kyushu, Japan.

620   Benthos Res 58(1):51–73. doi: 10.5179/benthos1996.58.1_51

621   Woodin SA, Wethey DS, Volkenborn N (2010) Infaunal hydraulic ecosystem engineers: cast of

622   characters and impacts. Integr Comp Biol 50(2):176–187. doi: 10.1093/icb/icq031

623   Wynberg RP, Branch GM (1994) Disturbance associated with bait-collection for sandprawns

624   (*Callianassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of

625   intertidal sandflats. J Mar Res 52(3):523–558. doi: 10.1357/0022240943077019

626   Yamada A, Somiya R, Ikeda N, Tamaki A (2017) The complete mitochondrial genome of the

627   burrowing ghost shrimp, *Nihonotrypaea harmandi* (Bouvier, 1901), (Crustacea, Decapoda,

628   Axiidea, Callianassidae) – a validation of the genus and species classifications. Mitochondrial

629   DNA B Resour 2(1):238–239. doi: 10.1080/23802359.2017.1318676

630   Yamada F, Kobayashi N (2007) Intertidal multiple sand bars in a low-energy environment. J Waterw

631   Port Coast Ocean Eng 133(5):343–351. doi: 10.1061/(ASCE)0733-950X(2007)133:5(343)

632   Yu OH, Soh HY, Suh H-L (2002) Seasonal zonation patterns of benthic amphipods in a sandy shore

633   surf zone of Korea. J Crustac Biol 22(2):459–466. doi: 10.1163/20021975-99990253

634   Zipperle A, Reise K (2005) Freshwater springs on intertidal sand flats cause a switch in dominance

635   among polychaete worms. J Sea Res 54(2):143–150. doi: 10.1016/j.seares.2005.01.003
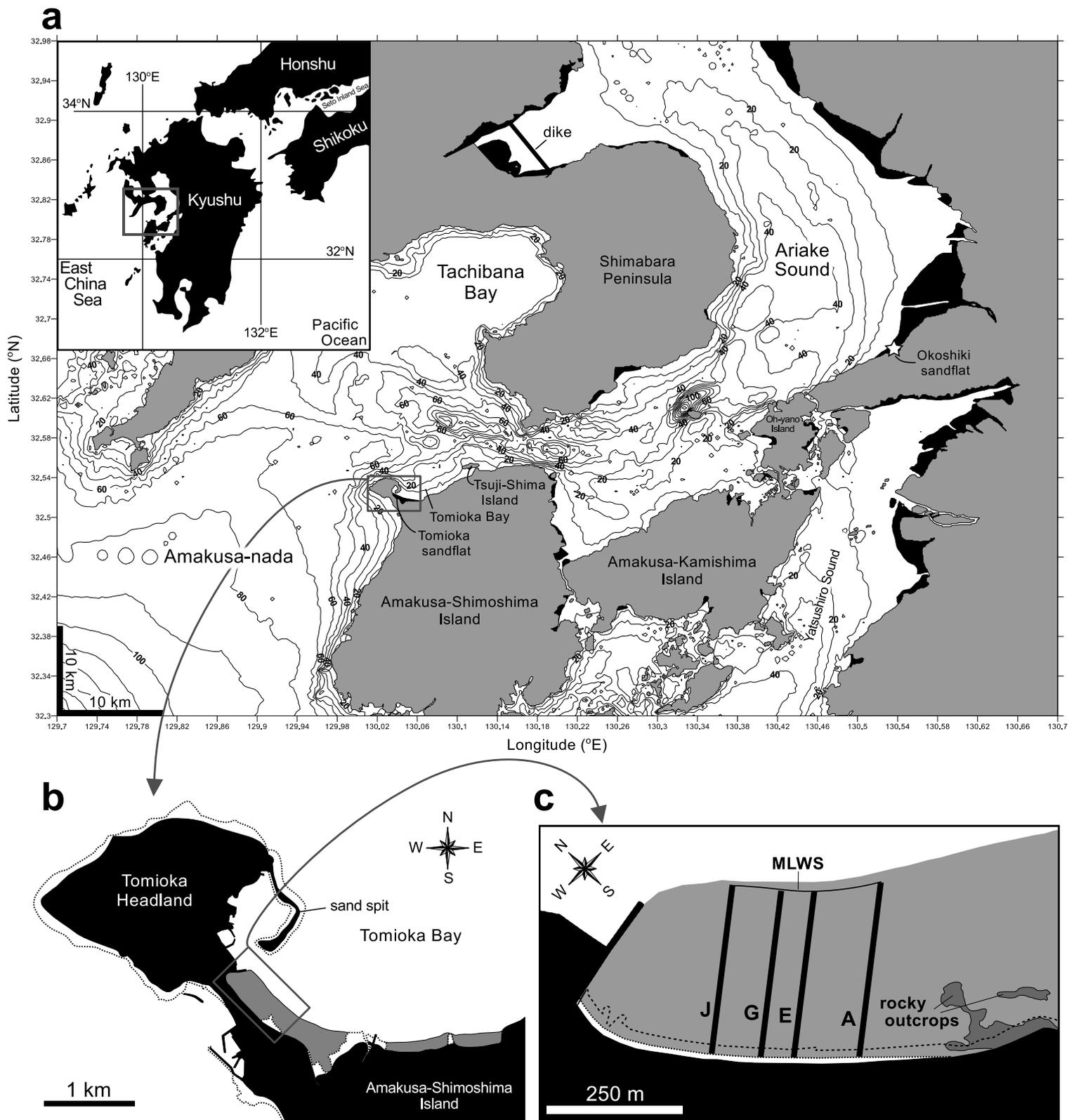
Fig. 1 a Study region and location of the Tomioka (intertidal) sandflat along the shoreline in mid-western Kyushu, Japan. Water-depth isopleths every 10 m were made by contouring (Surfer® 8: Golden Software, Inc.) for the point data provided by Hydrographic and Oceanographic Department, Japan Coast Guard. All tidal flats are indicated in black. The Okoshiki sandflat is situated in the middle part of Ariake Sound. **b** Enlarged map of the Tomioka sandflat. The intertidal sandy part and rocky or boulder part are indicated in light gray and white, respectively. **c** Four cross-shore transects (Transects A, E, G, and J) on the monitoring area of the Tomioka sandflat. The sandy part is indicated in light gray. The 10-m wide white-colored zone at the landward edge stands for the hard substrate in 1979–1991, from which the 20-m wide seaward zone down to the broken line was reclaimed during 1991 to 1993. MLWS: mean low water level in spring-tide periods
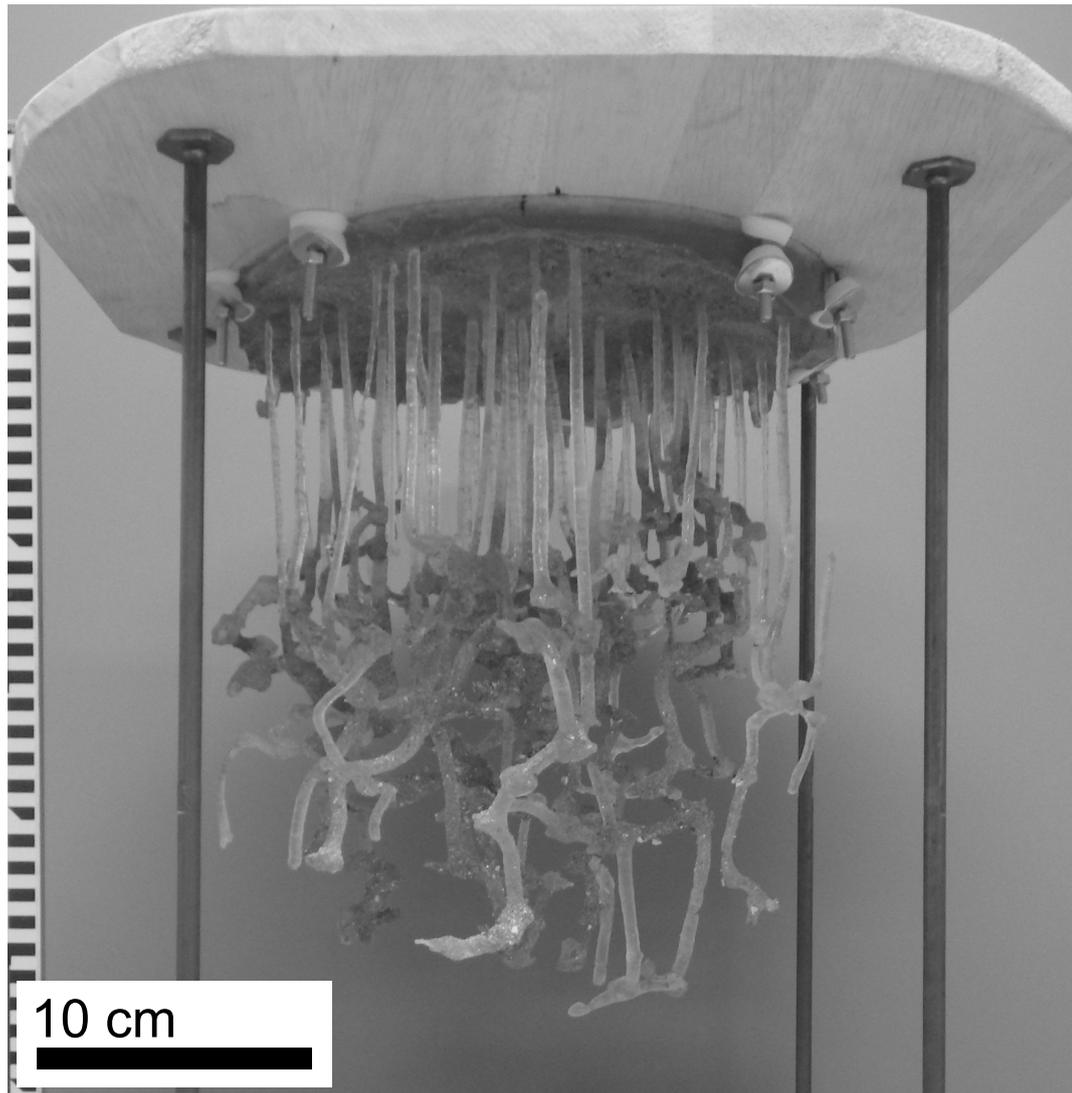
Fig. 2 Polyester resin casts of burrows of *Nihonotrypaea harmandi* made around the uppermost Tomioka sandflat during 27–28 May 2017
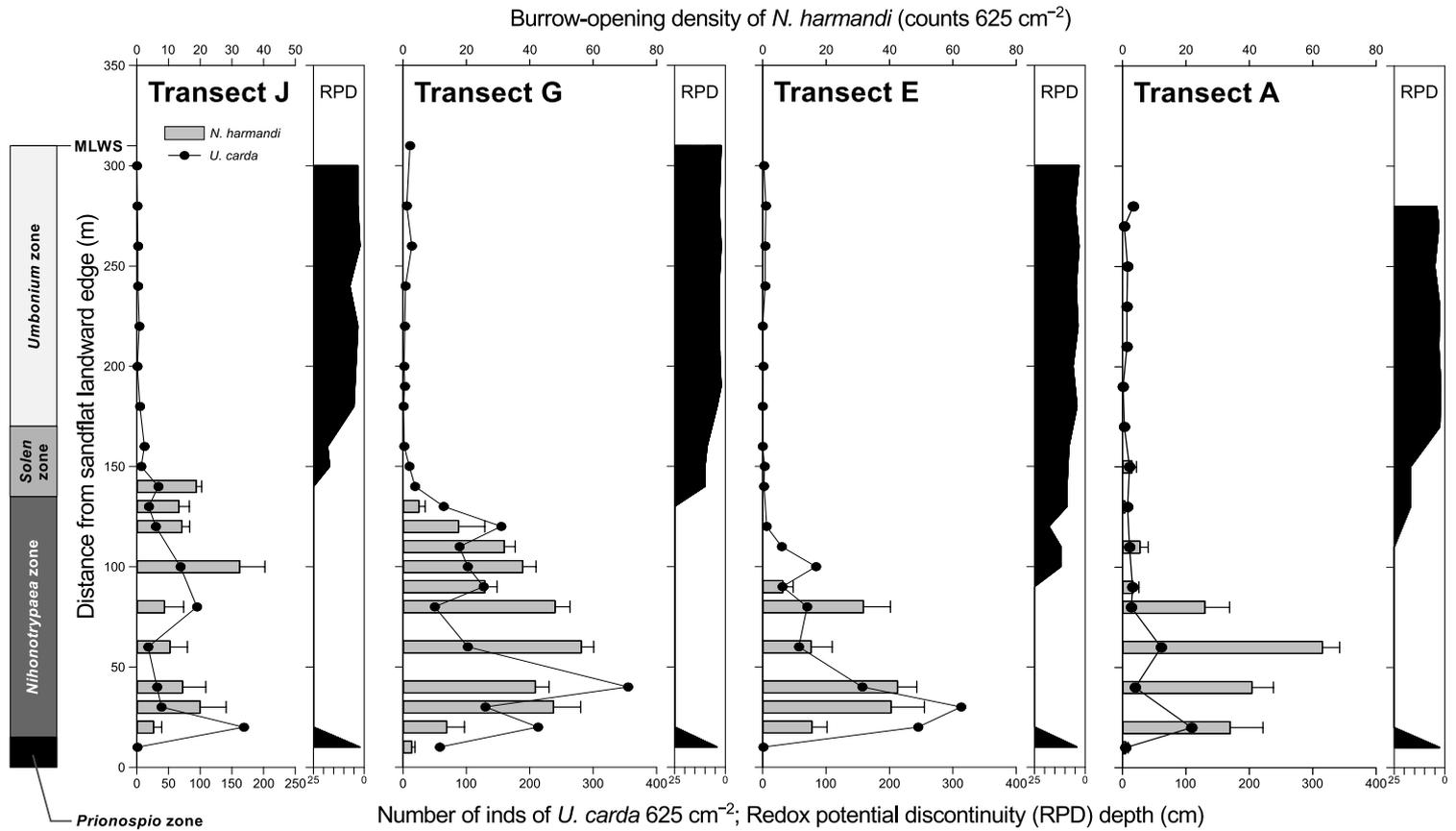
Fig. 3 Distribution of *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Nihonotrypaea harmandi*, and redox potential discontinuity (RPD) depths below the sediment surface along the four cross-shore transects on the Tomioka sandflat (Fig. 1c) on 10–11 August 1980. The numbers of 25- × 25-cm quadrat frame per station were one for *U. carda* and four for *N. harmandi*. Each RPD depth was determined as the thickness of the brown-colored layer (blank part in the panel) above the gray- or black-colored layers (black part), with the values ≥ 25 cm indicated uniformly as 25 cm. The four macrofaunal assemblage zones along Transect G are indicated on the left [designated by genera of representative species (Tamaki 1985)]. MLWS: mean low water level in spring-tide periods. The RPD values on Transect G based on data in Tamaki (1984)
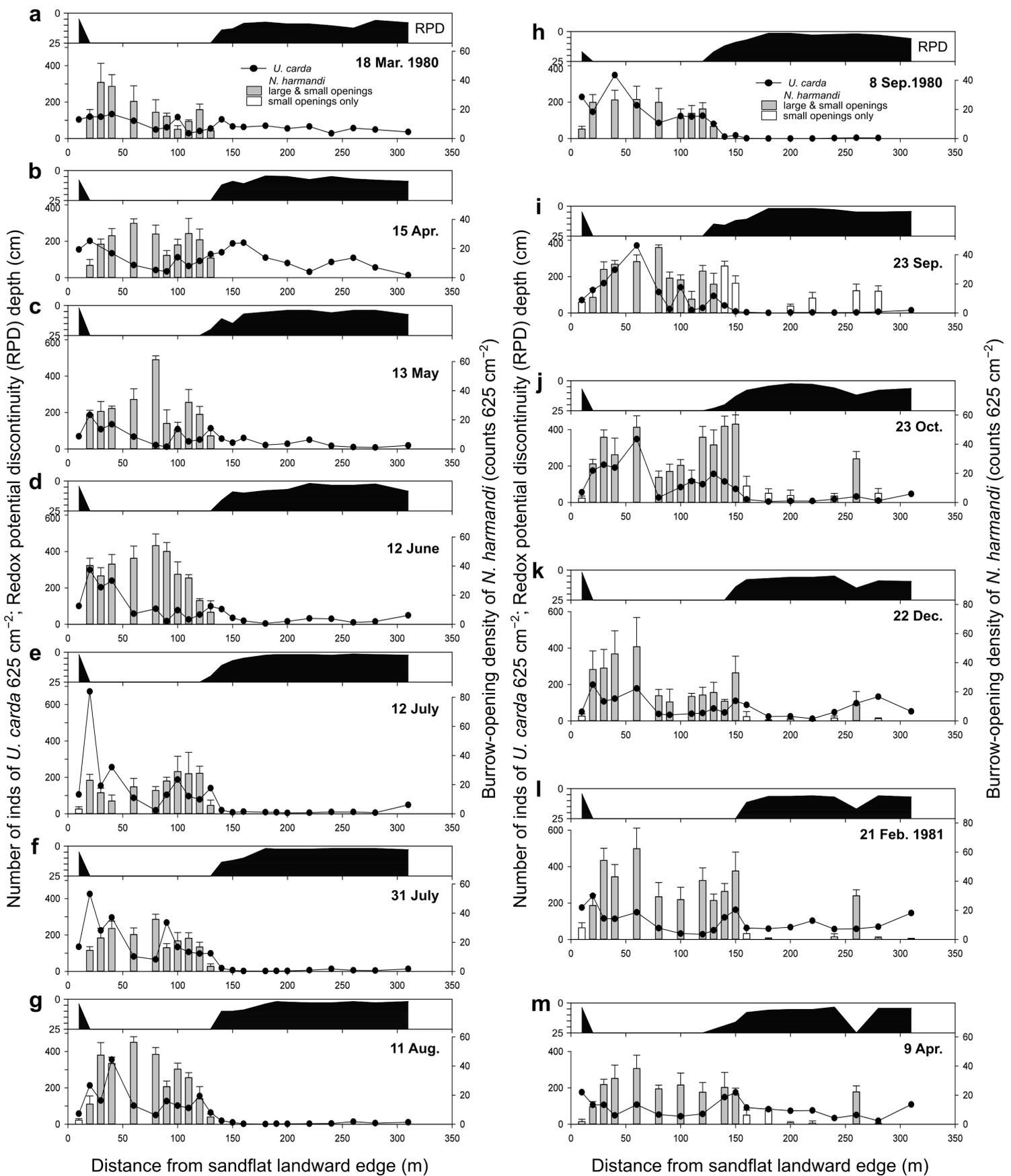
Fig. 4 a–m Spatial variations in *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Nihonotrypaea harmandi*, and redox potential discontinuity (RPD) depths below the sediment surface along Transect G on the Tomioka sandflat (Fig. 1c) during March 1980 to April 1981. The numbers of 25- × 25-cm quadrat frame per station were one for *U. carda* and four for *N. harmandi*. The stations with both large (3–6-mm φ) and small (1–2-mm φ) burrow openings and those with only small burrow openings are indicated by gray and blank columns, respectively. Each RPD depth was determined as in Fig. 3, based on data in Tamaki (1984)
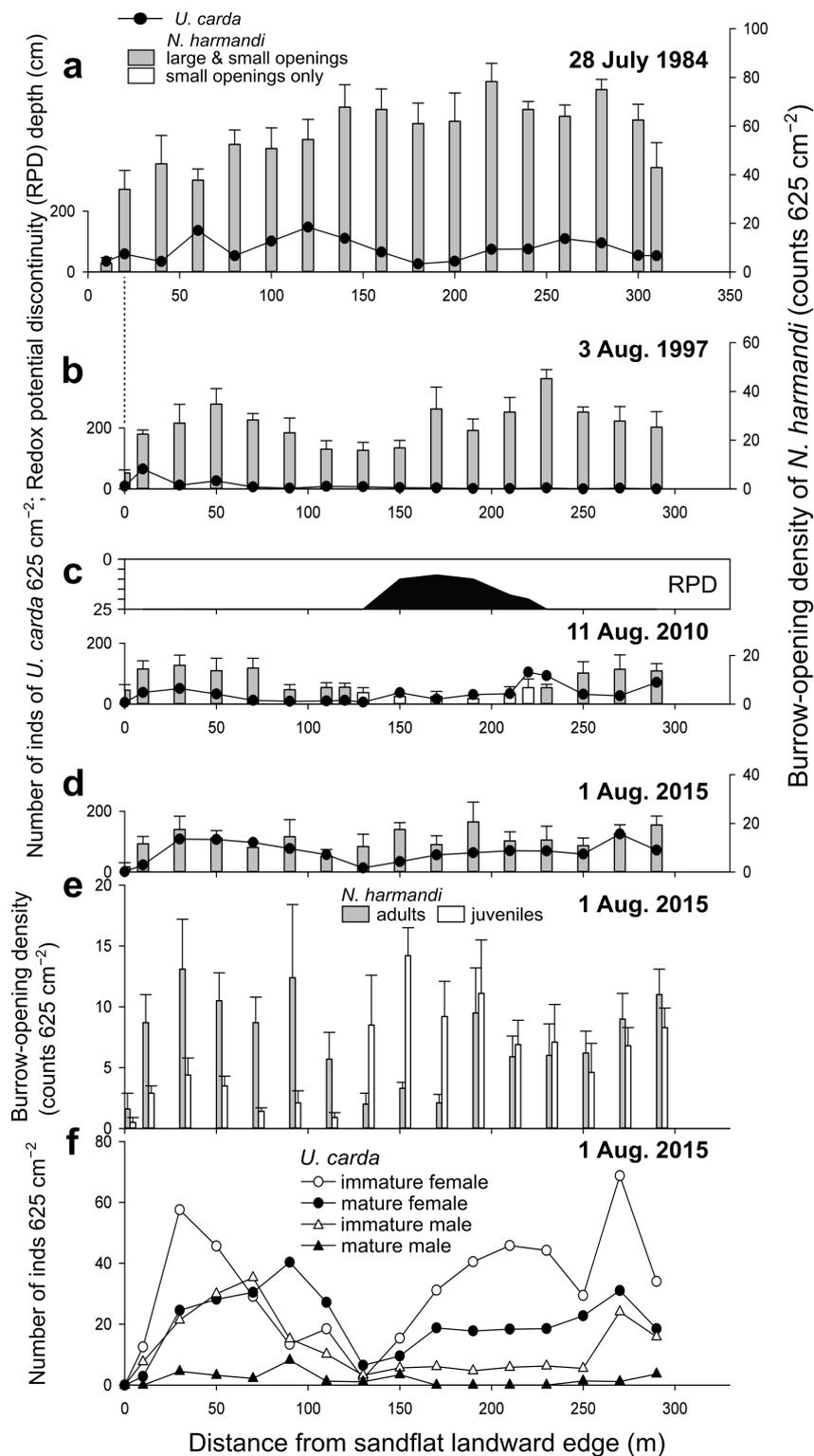
Fig. 5 a–d Spatial variations in *Urothoe carda* densities, mean (± SD) surface burrow-opening densities of *Nihonotrypaea harmandi*, and redox potential discontinuity (RPD) depths below the sediment surface along Transect G on the Tomioka sandflat (Fig. 1c) in late July to mid-August in 1984, 1997, 2010, and 2015. Note that the uppermost-shore station in 1997 to 2015 (Stn G-0) was the previous Stn G-20 (1980s). The numbers of 25- × 25-cm quadrat frame per station were one for *U. carda* and four (in 1984) and eight or nine (in 2010 or 2015) for *N. harmandi*. The stations with both large (3–6-mm φ) and small (1–2-mm φ) burrow openings and those with only small burrow openings are indicated by gray and blank columns, respectively. Each RPD depth was determined as in Fig. 3. In 1984, 1997, and 2015, the RPD depths at all stations except for the uppermost-shore station were ≥ 25 cm (not shown in **a, b, d**). **e** Mean (± SD) surface burrow-opening densities of adults and juveniles of *N. harmandi* along Transect G on 1 August 2015, as estimated from the total burrow-opening counts in **d** and the actual proportion of adults and juveniles in the coring tube samples collected on 3 August 2016. **f** Densities of the four groups (mature and immature individuals of each sex) of *U. carda* along Transect G on 1 August 2015. The total number of individuals at each station (**d**) was divided into these groups based on A. Tamaki et al. (unpubl data)
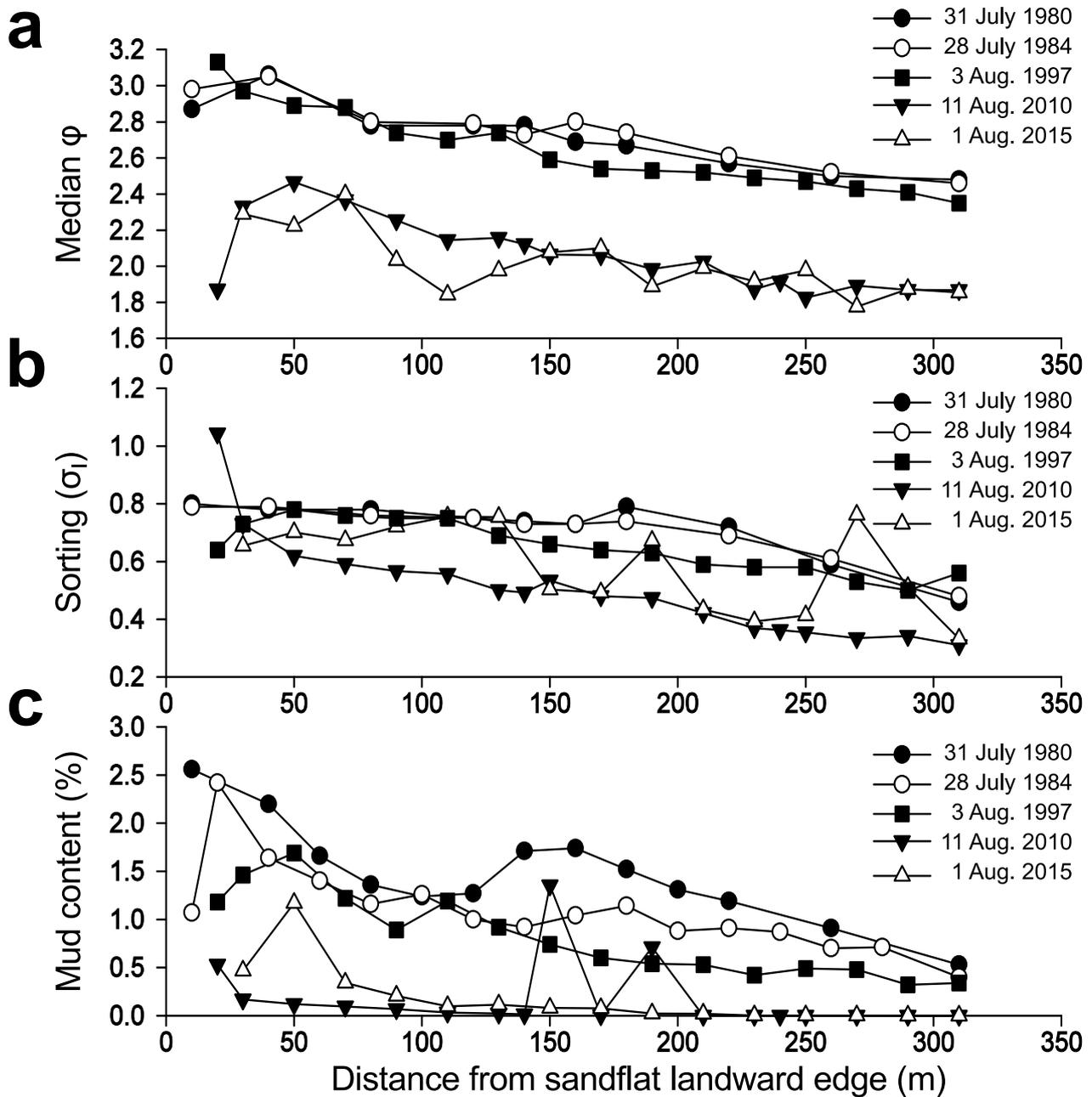
Fig. 6 a–c Spatial variations in median φ, sorting coefficient (σ$_I$: inclusive graphic standard deviation), and mud (= silt-clay) content of the surface 1-cm sediment along Transect G on the Tomioka sandflat in the summers of 1980, 1984, 1997, 2010, and the surface 3-cm sediment in 2015 (sample at Stn G-0 was lost). In 1980, the *Nihonotrypaea harmandi*-inhabited zone was from Stns G-20 to G-130, and from 1984 afterward, the whole transect was occupied by this species. The values in 1980 and 1984 based on data in Tamaki (1984) and Tamaki and Suzukawa (1991)
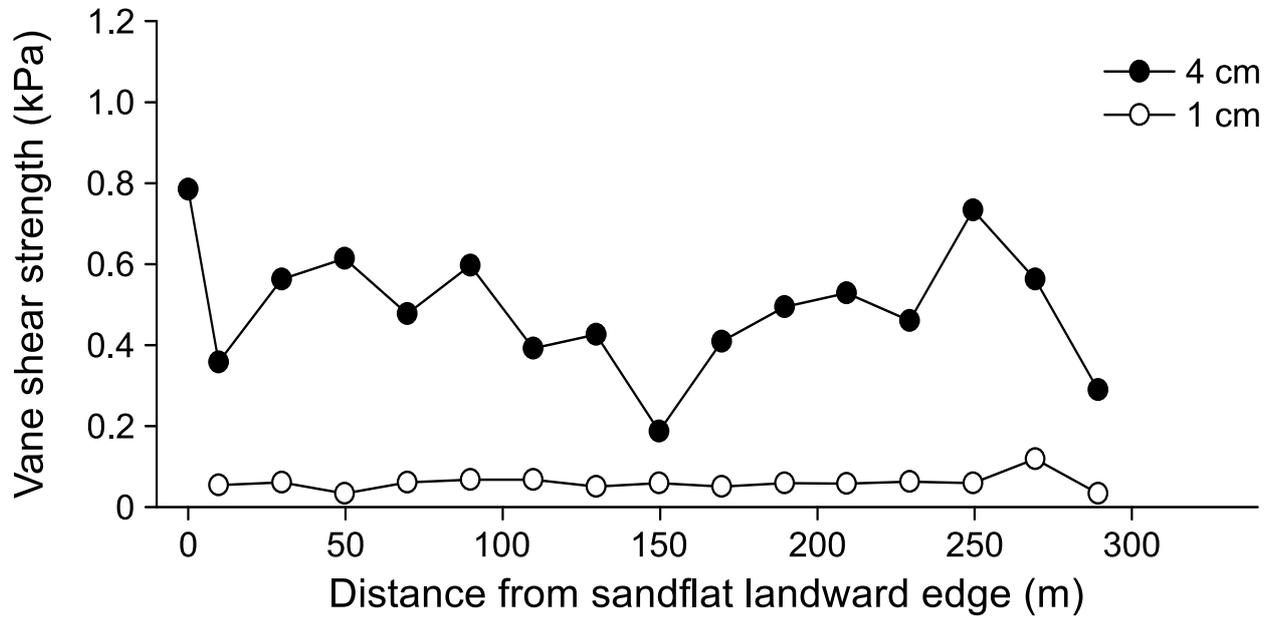
Fig. 7 Distributions of the vane shear strengths at 4 cm and 1 cm below the sediment surface outside *Nihonotrypaea harmandi* burrow openings along Transect G on the Tomioka sandflat during low tide on 1 August 2015
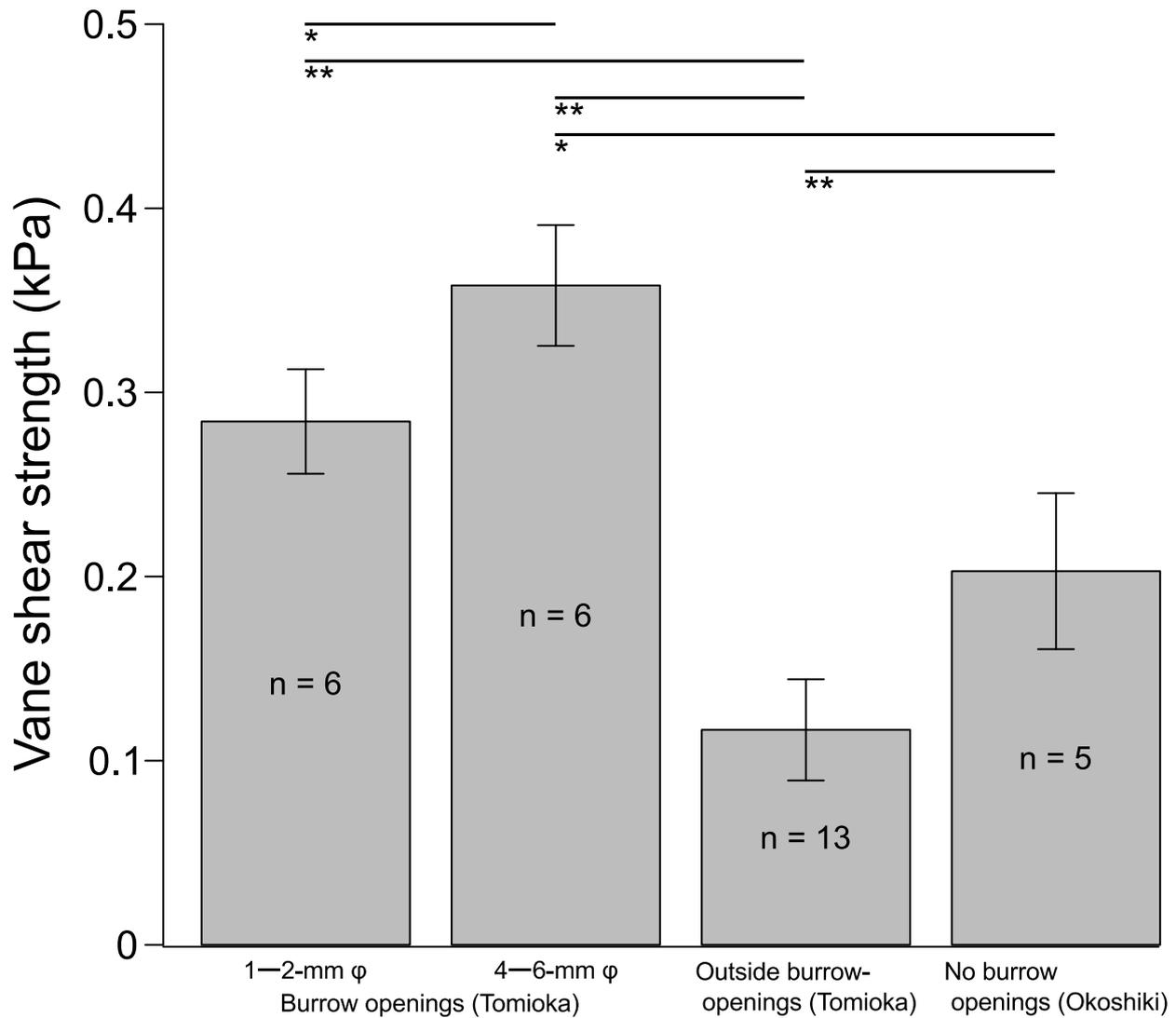
Fig. 8 Mean (± SD) vane shear strengths at 1 cm below the sediment surface at small *Nihonotrypaea harmandi*-burrow-opening points (1–2-mm φ), large burrow-opening points (4–6-mm φ), outside-burrow-opening points on the Tomioka sandflat during low tide on 1 August 2016 and on trough parts of sand waves with no burrow openings on the Okoshiki sandflat (Fig. 1a) during low tide on 14 June 2010 (from S. Sassa and S. Yang, unpubl data). Each pair with significant difference by Steel-Dwass multiple comparison test is indicated by * (0.01 < *P* < 0.05) and ** (0.001 < *P* < 0.01)