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<td>Author(s)</td>
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<td>Citation</td>
<td>Continental Shelf Research, 84, pp.139-157; 2014</td>
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<td>2014-08-01</td>
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Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sandflat

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Abstract

One notable type of bioturbation in marine soft sediments involves the excavation of large pits and displacement of sediment associated with predator foraging for infaunal benthos. Batoids are among the most powerful excavators, yet their impact on sediment has been poorly studied. For expansive temperate tidal flats, only relatively small proportions of the habitat can be sampled due to physical and logistical constraints. The knowledge of the dynamics of these habitats, including the spatial and temporal distribution of ray bioturbation, thus remains limited. We combined the use of aerial photogrammetry and in situ benthic sampling to quantify stingray feeding pits in Tomioka Bay, Amakusa, Japan. Specifically, we mapped newly-formed pits over an 11-ha section of an intertidal sandflat over two consecutive daytime low tides. Pit size and distribution patterns were assumed to scale with fish size and reflect size-specific feeding behaviors, respectively. In situ benthic surveys were conducted for sandflat-surface elevation and prey density (callianassid shrimp). The volume versus area relationship was established as a logistic function for pits of varying sizes by photographing and refilling them with sediment. This relationship was applied to the area of every pit detected by air to estimate volume, in which special attention was paid to ray ontogenetic changes in space utilization patterns. In total, 18103 new pits were formed per day, with a mean individual area of 1060 cm². The pits were divided into six groups (G1 to G6 in increasing areas), with abundances of G1, G2+G3, and G4–G6 being medium, high, and low, respectively. Statistical analyses using generalized linear models revealed a marked preference for the higher prey-density areas in G1 and the restriction of feeding grounds of G4–G6 to the lower shore, with G2+G3 being generalists for prey density and sandflat elevation. The lower degrees of overall bioturbation by G1 and G4–G6 were spatially structured for the eight sub-areas demarcated by prey density and sandflat elevation, while G2+G3 homogenized the state over the sandflat. The newly-formed pits’ sub-areal
mean numerical, excavated-areal, and displaced-sediment-volume densities per day were confined to small ranges: 0.14–0.17 m\(^{-2}\), 132–223 cm\(^{2}\) m\(^{-2}\), and 551–879 cm\(^{3}\) m\(^{-2}\) (latter two including 119 shallow non-pit excavations). These bioturbation rates are positioned at relatively high levels compared with those by rays from other geographic regions. The present procedure is applicable to the assessment of disturbance by any surface-sediment excavators on tidal flats if their pit dimensions are discernible from the air.

**Keywords:**

bioturbation; stingray; foraging; ghost shrimp; intertidal sandflat; aerial survey

1. Introduction

The excavation of large pits and displacement of corresponding amounts of sediment associated with predator foraging for infaunal macrobenthos or megaherbivore grazing on epibenthic vegetation are classic examples of bioturbation in marine and estuarine soft-sediment habitats (Bromley, 1996; Cadée, 2001; Hall et al., 1994; Meysman et al., 2006). In the marine bioturbator classification, these consumers are regarded as large epifaunal biodiffusors (Kristensen et al., 2012). This group includes vertebrates such as gray whale (Johnson and Nelson, 1984; Weitkamp et al., 1992), walrus (Oliver et al., 1985), sea otter (Hines and Loughlin, 1980), dugong (Preen, 1995; Skilleter et al., 2007), birds (Cadée, 1990; Nacken and Reise, 2000), sea turtle (Lazar et al., 2011) and demersal fish (Howard et al., 1977; Orth, 1975; Yahel et al., 2002), and invertebrates such as horseshoe crab (Botton, 1984; Woodin, 1978) and decapod crabs (Thrush, 1986; Woodin, 1978). The considerable modification of seabed topographies by these organisms is accompanied by sedimentological and biogeochemical
consequences for the ambient environment originally set by current and wave actions, such as
sediment and nutrient resuspension into the water column (Johnson and Nelson, 1984; Ray et al.,
2006; Yahel et al., 2008; Yahel et al., 2002), detritus accumulation in pits (Hall et al., 1991;
VanBlaricom, 1982), lateral transport of displaced sediment (Grant, 1983; Johnson and Nelson,
1984), and vertical mixing of this sediment in the substratum column (D’Andrea et al., 2004).

One major limitation to the assessment of high-magnitude epifaunal biodiffusors’ pit formation
and concurrent sediment displacement lies in the difficulty to cover a sufficiently large area of the
seabed with inherent spatial heterogeneity. Small-scale observations would not necessarily be
extrapolated to an unexplored larger area. For predators excavating feeding pits, the “total area”
needed for full assessment depends on the availability of information on pit size-frequency
distribution, density, local dispersion pattern, and landscape-scale distribution (Hall et al., 1994).
Sampling these areas in the field is constrained by low-tide times for intertidal assessments and to
scuba limitations for subtidal beds. Thus, these techniques generally cover relatively small
proportions of the seabed, between 50 and 26900 m² (Cadée, 1990; D’Andrea et al., 2004; Grant,
1983; Hall et al., 1991; Hines et al., 1997; Myrick and Flessa, 1996; Nacken and Reise, 2000;
O’Shea et al., 2012; Thrush, 1986; Thrush et al., 1991; VanBlaricom, 1982; Woodin, 1978). Several
attempts have been undertaken to cover larger areas. For a 20–40-m deep, 22000-km² bed of the
northeastern Bering Shelf, side-scan sonar was used to detect feeding excavations by gray whales
and walruses (Johnson and Nelson, 1984; Nelson et al., 1987; Ray et al., 2006). Aerial and/or
boat-based censuses have also been previously used to map epifaunal bioturbator impacts in shallow
subtidal beds with high water clarity. These methods have been applied to vegetation patches
resulting from grazing by dugongs in seagrass beds with up to a 110-km² area (Preen, 1995) and
from cownose ray digging in eelgrass beds up to a 24-ha area (Hovel and Lipcius, 2001; Orth, 1975)
and pits formed by stingrays in a 1-km² lagoon (O’Shea et al., 2012). Aerial surveys have been least
used for intertidal zones, with only one study of gray whale pits along a 90–180-km stretch of Puget Sound shoreline in Washington, U.S.A. (Weitkamp et al., 1992) and another on horseshoe crab pits by digital camera moving along a 50-m long cable (Lee, 2010).

Of the demersal fish epifaunal biodiffusors in soft-sediment habitats, rays (Chondrichthyes: Batoidea) are among the most powerful excavators that can make large pits (e.g. 1-m wide and 10s-cm deep) as they prey on deep-dwelling infauna from sandy substrate (Cadée, 2001; Kristensen et al., 2012). Preys are mined hydraulically by jetting water from the mouth or gills (Gregory et al., 1979; Sasko et al., 2006). Prey targeted in these habitats vary among ray taxa; cow-nose rays and eagle rays generally select bivalve mollusks (Ajemian et al., 2012; Hines et al., 1997; Peterson et al., 2001), while stingrays favor decapod crustaceans and fish (Ebert and Cowley, 2003; Howard et al., 1977; Taniuchi and Shimizu, 1993; Tillett et al., 2008). Some studies suggest that density-dependent foraging behaviors of rays could stabilize local prey populations (Ajemian et al., 2012; Hines et al., 1997) and bring about prey metapopulation source–sink dynamics (Peterson et al., 2001).

Two measures associated with ray pit excavations have been considered as their basic bioturbation rates: (1) numerical density and distribution of newly-formed pits with various horizontal and vertical dimensions and (2) volumetric density and distribution of sediment displaced aside newly-formed pits. To date, only a handful of estimates have been presented for these measures, which were generally extracted from a small portion of each study site (Cross and Curran, 2004; D’Andrea et al., 2004; Grant, 1983; Hines et al., 1997; Myrick and Flessa, 1996; O’Shea et al., 2012; Reidenauer and Thistle, 1981; Sherman et al., 1983; Thrush et al., 1991; Valentine et al., 1994; VanBlaricom, 1982). It is only after the proper assessment of these bioturbation rates that the subsequent processes of lateral transport of discarded sediment and vertical mixing in the substratum column can be evaluated (D’Andrea et al., 2004; Myrick and Flessa, 1996). Aerial methods can be a strategic tool to help enlarge the survey areas that likely contain high spatial heterogeneity in each
habitat type, especially within intertidal zones that have limited access due to tidal activity. The ray
bioturbation rates can vary spatially, depending on the physical setting of feeding grounds and the
prey-density distribution. Physical components of heterogeneity in intertidal zones include: thickness
of sediment column in which deep-dwelling benthic prey can escape from surface disturbance, and
surface topographic elevation. The latter component is particularly relevant to high-tide predators
like stingrays, which access this zone from the subtidal region and are thus at risk of being stranded
with receding tides. Regarding the influence of prey abundance, only Hines et al. (1997) described a
spatially varying prey-density-dependent pit-excavation rates for eagle rays. Finally, for estimating
the volume of displaced sediment from pits, semi-ellipsoid or inverted-cone approximation to pit
shape has sometimes been made, with circular or elliptical area and maximum depth given (Cross
and Curran, 2004; D’Andrea et al., 2004; O’Shea et al., 2012), but more reliable estimates can be
obtained by direct refilling of pits (Myrick and Flessa, 1996).

Long-term observations (1979–2001) of the benthic community on an intertidal sandflat in
Amakusa-Shimoshima Island, western Kyushu, southern Japan (Fig. 1) indicated an abrupt increase
in pits formed by the stingray, *Dasyatis akajei* (Müller & Henle) from 1995 (Flach and Tamaki,
from the four prefectural governments surrounding Ariake Sound adjacent to the present study area,
Yamaguchi (2005) summarized trends in the abundance of rays and sharks in the sound: (1) rays
increased steadily to reach a maximum during 1988 to 1995 and thereafter decreased to a level
which was still higher than those before 1985, (2) *D. akajei* accounted for most of these rays, and (3)
sharks decreased largely continuously to 1997, with a subsequent slight increase. In Amakusa, the
stingray almost exclusively forages on ghost shrimp (*Decapoda: Axiidea: Callianassidae*),
*Nihonotrypaea harmandi* (Bouvier), the most dominant species in biomass in the benthic community
(Flach and Tamaki, 2001; Harada and Tamaki, 2004). In other parts of the world, ghost shrimps
co-occur with ray pits in intertidal-flat habitats (D’Andrea et al., 2004; Martinell et al., 2001; Myrick and Flessa, 1996) and are reported to be a major prey item for dasyatid stingrays (Ebert and Cowley, 2003; Howard et al., 1977; Tillett et al., 2008). In Amakusa, the decline of the ghost shrimp population occurring since 1995 has been attributed to increased predation pressure by *D. akajei*, which has induced cascading effects on other members of the benthic community (Flach and Tamaki, 2001; Harada and Tamaki, 2004; Mandal et al., 2010). A similar chain of events originally caused by *D. akajei* population increase was recently documented for an intertidal sandflat community in Ariake Sound (Takeuchi et al., 2013). However, pit-related bioturbation rates on the sandflat in Amakusa remain to be quantified except for some preliminary data (Harada and Tamaki, 2004); until around 2000, the manual census of stingray feeding pits during low-tide hours was not entirely impossible at least for a narrow strip along tidal gradient. Most recently, this is no longer feasible due to the overwhelming pit density.

The first objective of the present study was to construct digitized maps of newly-formed stingray pits over an 11-ha section of the above intertidal sandflat in Amakusa. As the most basic premise of the study, pit size and distribution patterns were assumed to scale with fish size and reflect size-specific feeding behaviors, respectively (Hall et al., 1994; Hines et al., 1997). Following the result of a pilot aerial survey, a main aerial survey over two consecutive daytime low tides was performed to detect pits formed in one day. At the same time, benthic surveys were conducted for sandflat-surface elevation profile, sand-column thickness, and ghost shrimp density. Furthermore, the maximum-depth–area and volume–area relationships were established for pits of varying sizes by photographing excavations and refilling them with measurable quantities of sediment on the ground. These relationships were applied to the area of every pit detected by air to estimate its maximum depth and volume, in which special attention was paid to the stingrays’ ontogenetic change in their space utilization pattern with regard to ghost shrimp density and sandflat elevation.
Finally, an assessment was made on spatial variation in numerical density, excavated-area density, and estimated displaced-sediment-volume density of pits per day over the sandflat, and the mean values for these bioturbation rates were compared with those obtained or estimated for ray pits from other geographic regions.

2. Materials and methods

2.1. Study site and benthic community

The intertidal sandflat is located in a shallow sub-embayment of Tomioka Bay situated on the northwestern corner of Amakusa-Shimoshima Island in western Kyushu, Japan (Tomioka sandflat; 130°02'E, 32°31'N; Fig. 1A–C). The sediment of the sandflat is moderately well-sorted fine sand, with 0.3–1.7% silt-clay content (Wardiatno et al., 2003), and with relatively small ripples (Fig. 2B: wave length, 6–11 cm and wave height, 1–1.5 cm; Tamaki, 1984). The waters around Tomioka Bay are under a mesotidal, semidiurnal tidal regime, with the average tidal range of 3 m during spring tides. The sandflat is exposed for a maximum of 150–550 m seaward and 4 km alongshore. Tomioka sandflat faces north–northeast, receiving northerly wind-induced waves from October to May but minimal wave action in the summer months due to prevailing southwesterly winds (Tamaki, 1984, 1987). The aerial survey domain was affixed to a 107516-m² northwestern edge section of the sandflat with a 540-m alongshore length (Fig. 1D). The water-level change was recorded at a middle point in the domain during the main aerial survey period at a spring tide (17–18 August 2012) using a water-pressure gauge (Wave Hunter 99, IO Technic, Co.; sensor positioned 1.4 cm above the sandflat surface and recorded measurements every 0.5 seconds). To remove any noise associated with very shallow depths, pressure data less than 30 gw cm⁻² (≈ 2.94 kPa; hereafter, “gw cm⁻²” will be used) were eliminated from analysis (see Yamada et al., 2009). The maximum and mean
flood-current speeds were 130.7 and 6.1 cm s\(^{-1}\) and those for ebb currents were 110.9 and 4.2 cm s\(^{-1}\), respectively. The waves were weak, with a significant height of 3.4 cm, which would not have caused rapid changes in the sandflat micro-topography (A. Tamaki, personal observation). The substratum column of the sandflat was composed of 30–60-cm sand portion inhabited by *Nihonotrypaea harmandi*, and a bed of shell (both bivalve and gastropod) remains in the lower layer (Flach and Tamaki, 2001; Tamaki and Ueno, 1998). The shell bed formation could partly be attributed to ghost shrimp biogenic stratification (Myrick and Flessa, 1996; Wardiatno et al., 2003).

Since 1979 the change in benthic community has been monitored by A. Tamaki and colleagues twice per year for a 300-m × 300-m northwestern portion of the sandflat, which was included in the present aerial survey domain. During summer, the daytime lowest tides at spring tides take alternate higher and lower levels every two weeks. The main survey time of 2012 was at a higher water level, and the sandflat was exposed for a distance of 240 m seaward. The distance was extended 20–60 m further during the spring tide of the pilot survey time of 2011.

In 1979, the *N. harmandi* population occupied the higher one-third zone of the sandflat, and expanded its distribution to encompass the entire intertidal region by 1983 (Tamaki and Ingole, 1993). Pits of the stingray, *D. akajei*, rapidly increased in 1995, and have been a persistent topographic feature of the sandflat from June to October in subsequent years, with peak occurrence from the end of June to mid-September; the rays found by enclosing a large portion of the sandflat until its exposure were *D. akajei* only (Harada and Tamaki, 2004; A. Tamaki, unpublished data). The period of occurrence of stingrays coincides with the reproductive season of *N. harmandi*, in which water temperatures are above 20°C (Tamaki et al., 1997).

2.2. Stingray foraging characteristics

Previous research for stomach and gut contents of *D. akajei* specimens collected from the
Tomioka sandflat has shown that rays from 14 to 60 cm in disc width ingested *N. harmandi* over the full size range of the population from 4 to 42 mm in total length (Harada and Tamaki, 2004). On the sandflat, newly-formed stingray pits are refilled with surrounding sediment usually in 2–5 days, depending on pit size and hydrodynamic conditions (Harada and Tamaki, 2004). Any snapshot of the sandflat surface comprises a mixture of pits with various ages and therefore, to identify the newly-formed pits (i.e. < 1 d), surveys over at least two consecutive dates were required.

The stingray pits observed on the Tomioka sandflat can be grouped into two major types: (1) a single semi-ellipsoidal pits (Fig. 2A; Grant, 1983; Howard et al., 1977; Myrick and Flessa, 1996), and (2) a complex of one deep, semi-ellipsoidal pit and an associated shallow, sinuous furrow (Fig. 2B). The latter morphology is sometimes found in isolation. These furrow characteristics have not been reported for any other ray species’ pits. We supposed that (1) prey search by stingrays initially involved shallow excavations with pectoral fins to form a sinuous furrow and (2) once the target patch was determined, the ray forcefully excavated a deep pit by hydraulically jetting water from its mouth or gills (Gregory et al., 1979; Sasko et al., 2006), leaving a semi-ellipsoidal scar (hereafter termed feeding pit; when either deep, feeding pit or shallow, sinuous furrow alone and their complex are collectively referred to, these are termed foraging traces). We also supposed that isolated sinuous furrows were signs of aborted foraging bouts. The observation that smaller feeding pits were mostly unassociated with sinuous furrows suggests the absence or insignificant force for the initial prey search by smaller stingrays. When approximated to an ellipse on the horizontal plane of the sandflat, the feeding-pit minimum dimensions were ca. 20 cm in long axis and 15 cm in short axis. Any quantitative relationships between depth or volume and area can be used to identify newly-formed foraging traces during manual surveys on the sandflat. Fresh sediment mounds displaced aside feeding pits and sinuous furrows can be another clue for inferring them as newly formed (e.g. signs of lower degrees of sediment dispersal by tidal currents; Fig. 2A,B).
2.3. Aerial survey methods and mosaic imaging

Aerial-based detection of newly-formed stingray foraging traces required knowledge of the exact geographic overlap of the corresponding photographs. In August, 2012, we obtained a set of two consecutive dates’ color ortho-projected images over the sandflat following standard aerial photogrammetry. The methods employed in the survey are detailed further in the Appendix 1.

2.4. Treatment of newly-formed stingray foraging traces on the mosaic images

Tracing the outlines of newly-formed stingray foraging traces on the above-obtained mosaic images was conducted on two displays [Flex Scan SX2762W (27 inch in size) or S2402W (24 inch), ElZO, Co., Ltd.], using GIMP 2.8.2 [http://www.gimp.org/downloads/ (accessed on 9 January 2014)] drawing freeware. The two dates’ mosaic images were displayed as separate layers for detecting the newly-formed foraging traces. Due to file-size limitations for practically handling a single image (up to 8 Mb), the mosaic image for each date was divided into 320 sub-images each with 2000 × 2000 pixels, using the freeware OpenCV 2.4.1 library [http://opencv.org/ (accessed on 9 January 2014)]. The feeding pits and sinuous furrows were recognizable by their darker inside colors (due to the presence of water) than outside and, for large newly-formed pits in particular, by lighter sediment mounds displaced to the side (Fig. 2C–G). The detected newly-formed pits and furrows were displayed in a one-tenth their actual sizes on a new layer, traced, and output as 8-bit RGB color images with the same resolution as in the original mosaic images. Feeding pits and sinuous furrows were discriminated by shape (elliptical versus irregular) and traced separately. The junction between pit and furrow was drawn by smoothly extrapolating from the free part of the feeding pit as an ellipse and closing it (Fig. 2C,E).

The area of each feeding pit or sinuous furrow was measured with a freeware, ImageJ 1.46r.
in which the total number of 3.24 (= 2.41 + 1.82)-cm² component pixels was enumerated. The measurement error in area for a smallest stingray-pit equivalent was assessed by measuring the area of each of 24 arbitrarily chosen “marker-points” for aerial photogrammetry (for marker points, see Appendix 1 and Fig. 1D; 20-cm × 20-cm square boards were used; 14 from the southern part of the survey area on the first day and 10 from the northern part on the second day). For the procedure hereafter, the RGB color image was transformed into an 8-bit gray-scale image with 256 pixel values; the feeding pit and the sinuous furrow were given different specific colors. Then further binarization (1 versus 0) was applied to the feeding pits versus the others and to the sinuous furrows versus the others, respectively. Finally, the members of the feeding-pit group and those of the sinuous-furrow group were labeled respective serial numbers, in which all component pixels of each member were given an identical number. To avoid lumping two feeding pits that were partially touching, the watershed segmentation had beforehand been made for all pits, using Watershed command in ImageJ. The representative geographic coordinate position for each of the feeding pits and sinuous furrows on the ground was defined as the means for all component-pixel positions.

2.5. Estimation of volume of sediment displaced by stingray foraging

To estimate the volume of sediment displaced by stingray foraging for each excavated area measured on the aerial ortho-projected images, the volume–area relationships had to be established based on data acquired by hand for feeding pits and sinuous furrows on the sandflat. The direct infilling of these foraging traces was conducted during low tides on eight dates under calm weather and sea conditions in the period from 14 September to 17 October 2012. Previous research has shown that feeding pits tend to deepen with area; for newly-formed pits, the upper and lower envelope curves for the scatter plots of maximum depth (D, cm) versus area approximated to an
ellipse in plane shape \((A, \text{ m}^2)\) are given as \(D = 0.7 \times (10^4 A)^{0.3}\) (upper; maximum \(A = 1.79\)) and \(D = 5.0 \times \ln (10^4 A) - 35.3\) (lower; maximum \(A = 2.13\)) (A. Tamaki et al., unpublished data). The main causes for the generation of a rather wide range in both maximum depth and area are the differences in the time of pit formation within one day with two high tides and in the wave conditions. The above equations can primarily be referred to for the identification of newly-formed pits in situ.

Finally, a total of 35 newly-formed feeding pits and 17 associated sinuous furrows were selected on the sandflat. For the feeding pits, the lengths of major axis, minor axis, and maximum depth were measured to the first decimal place in cm. For depths of the sinuous furrows, measurements were made on 1–19 points per furrow along the central part of its winding path. The feeding pits and sinuous furrows were photographed from 2 m above, using a digital camera (Optio WG-2, RICOH, Co., Ltd.) secured on the top edge of a reverse L-shaped pole, with the shutter released remotely. The acquisition of ortho-projected images was assured by monitoring a level attached to the vertical part of the pole. At least four markers were arranged along the edge of pits or furrows per image, with a 70-cm long graduated (to 1 cm) staff placed aside as a scale. In the cases in which the sinuous furrow was associated with the feeding pit, their junction was demarcated by several markers. For the larger feeding pit and sinuous furrow complexes (\(\geq\) ca. 1.5 m\(^2\) in total area), it was impossible to capture the entire outline within one image. In such cases, the subdivided images were taken. The infilling of feeding pits and sinuous furrows was conducted separately, into which nearby sediment was poured with measuring cups. The sediment lumps put inside the pit and the furrow were leveled off with a trowel to be finally flush with the surrounding sandflat surface, when the sum total volume was determined to 100 cm\(^3\).

In the laboratory, the above-treated subdivided images were combined into one image on the computer display, automatically with a freeware, Microsoft Image Composite Editor 1.4.4.0 [http://research.microsoft.com/en-us/um/redmond/groups/ivm/ice/ (accessed on 9 January 2014)] or
manually with Microsoft Office PowerPoint 2007. Each feeding pit and sinuous furrow was traced along its outline, divided into pixels, and measured for area with reference to the scale staff, using ImageJ. For the feeding pits, maximum depth or volume was regressed against area using linear, power, and logistic models, of which the best-fit ones were selected based on Akaike’s Information Criterion (AIC; Akaike, 1973). For the sinuous furrows, a similar analysis was made on volume–area relationship. These regression equations were used to estimate the maximum depth and the volume for all area-measured newly-formed pits and sinuous furrows that had been identified by comparing the two dates’ aerial mosaic images.

The spatial variation in the numerical, areal, and volumetric densities of the newly-formed stingray foraging traces over the sandflat was examined using 10-m × 10-m unit grid cells. The entire area of the aerial survey was divided into 934 complete cells and 267 irregular-shaped marginal cells (polygons). The smallest marginal cells with area < 1 m² (N = 14) were excluded from analysis, as they could bring about extremely high numerical density values when converted to the 100-m² unit [e.g. 292.1 for a 0.34-m² marginal cell versus 59.0 (maximum) and 17.1 ± 7.3 (mean ± SD) for all complete cells; the latter two values for all complete cells and those remaining marginal cells inclusive were 59.0 and 16.5 ± 8.4, N = 1187]. For each cell, the densities of the excavated area (cm² m⁻²) and displaced-sediment volume (cm³ m⁻²) were calculated by summing the values for all feeding pits and sinuous furrows that were contained there. For graphic representations, the densities were classed by either Quantile or Natural Breakes (Jenks) modes, using Quantum GIS 1.8.0 (Quantum GIS Development Team, 2012).

2.6. Numerical density of ghost shrimps and sand-column thickness on the sandflat

Ghost shrimp density was surveyed over the sandflat during low tides on 30 June and 1 July 2011 (at 120 points in total), 3 and 4 July 2012 (138 points), and 21 and 24 July 2013 (39 points),
with concomitant measurement of sand-column thickness conducted in 2012. The positions of the
survey points were recorded with hand-held GPSs (Global Positioning Systems, eTrex Venture HC
and Geko 201, Garmin, Co., Ltd.). The ghost shrimp density at each point was estimated based on
burrow-opening counts in two 50-cm × 50-cm plots, as a single individual of *N. harmandi* dwells in
a Y-shaped burrow with two surface openings (Tamaki and Ueno, 1998). The plots at each point
were chosen haphazardly from a relatively flat part of the nearby sandflat surface, with areas
showing apparent signs of recent excavations avoided. The sand-column thickness was measured
through the above-ground length of a 120-cm long stiff rod (10-mm ϕ) which was penetrated into
the sediment to its basal shell bed. In the laboratory, geostatistical analyses for the above parameters
were performed using “R” (R Core Team, 2012). The minimum area that covers all survey points for
spatial interpolation (= convex hull) was determined using “chull” function. The convex hull was
divided into 2-m × 2-m unit grid cells with each representative point positioned at its center. The
values of ghost shrimp density and sand-column thickness for all cells were interpolated following
the ordinary Kriging, in which the variogram model was constructed using “variofit” function in
“geoR” package (Ribeiro and Diggle, 2001) and the interpolation made using “krige.conv” function.
In “variofit” function, “gaussian” was adopted as the “cov.model” argument.

### 2.7. Difference in foraging ranges by stingray size

To characterize foraging ranges by stingrays of the different size groups on the sandflat, a fixed
kernel method (Worton, 1989) used for home range analysis in biotelemetry research (e.g. Beisiegel
and Mantovani, 2006; Villegas-Rios et al., 2013) was applied to the 2012 aerial-survey data set on
feeding-pit geographic coordinates. In the present study, by “home range” is meant the spatial extent
of the main feeding-pit distribution range for each size group, and the 50% home range (core home
range) and 95% home range (home range extent) were estimated. This home range is different from
that in its ordinary usage [see Cartamil et al. (2003) and Tilley et al. (2013) for stingray examples],
but the technique is applicable to the present case. The feeding pits were divided into six groups
according to their areal ranges [G1 (= Group 1)–G6; see Section 3.3]. The determination of the two
home ranges was made using “getverticeshr” function in “adehabitat” package (Calenge, 2006) run
in “R” (R Core Team, 2012), with “lev” arguments in the function set at 50 or 95.

2.8. Difference in foraging sites by stingray size according to prey density and sandflat elevation

To detect any selectivity of stingrays of the different size groups (as reflected on the G1–G6 in
their pit areas) for prey (ghost shrimp) density and/or sandflat elevation, a generalized linear model
(GLM) fitting was performed using “R” (R Core Team, 2012). A random-point data set was made
against the 2012 data set of all observed points (throughout G1–G6) in the (x, y)-geographic
coordinate. The observed points, with respective feeding-pit areas, were labeled the serial numbers.
Using “csr” function in “splancs” package [http://CRAN.R-project.org/package=splancs (accessed
on 9 January 2014)], a set of completely random points was generated, with their total numbers the
same as for the observed points. Any random point with its serial number identical to that of a
specific observed point was assigned the same Gn. The random-point data set in the coordinate for
each of the G1–G6 was used as the case for no selections for ghost shrimp density and/or sandflat
elevation by stingrays. The ghost shrimp density and sandflat elevation at each observed feeding-pit
point and random point were read from the result of the Kriging interpolation for the shrimp-density
record in 2012 and the digital elevation model (DEM; see Appendix 1 for details), respectively,
using “overlay” function in “sp” package (Pebesma, 2004). The original DEM was modified into a
2-m mesh model, which was coarser in spatial resolution but sufficient for the present analysis. The
spatial range for the ghost-shrimp density census was shorter by ca. 90 m in alongshore length than
in the aerial survey range, and the analysis was made for their overlapped part.
In the GLM fitting procedure for each of the G1–G6, the explanatory variables were prey density and sandflat elevation, and the binary response variable was set to take the values of 1 for the observed points and 0 for the random points. The value of the response variable at any point on the geographic coordinate indicates the probability for this point to be a feeding pit. Four GLMs were fit to the response variable, with prey density alone (Model 1), sandflat elevation alone (Model 2), both (Model 3), and null (= indifferent to both; Model 4) used as explanatory variables, assuming a binomial probability distribution for each. The best-fit model was selected based on AIC. The fitness of the models can vary according to random-number sets which are generated differently from run to run in “csr” function. Thus, to examine which of the four models had the highest probability of occurrence as best fit, the generation of random points and subsequent model selection was repeated 99 times.

2.9. Pilot aerial survey methods and mosaic imaging

A pilot survey with the use of an unmanned helicopter was conducted to confirm the detectability of stingray foraging traces by aerial photography on 31 July 2011 under sunny and calm conditions. A result of this survey was used here to fill a gap of data on stingray foraging traces on the lowest shore that was not covered in the 2012 aerial survey [i.e. between the seaward edge of the white part and the blue line (mean low water level at spring tides) in Fig. 1D]. The methods employed in the survey are detailed further in the Appendix 2.

In the laboratory image processing, the whole sandflat was divided into 23 sub-areas each with ca. 95 m in alongshore length \( \times \) ca. 65 m in shore-normal length. For each sub-area, the component images were combined into one image, using “photomerge” function of an image editor (Photoshop CS4 11.0, Adobe Systems, Inc.), over which a lattice of longitudes and latitudes to the second was drawn based on the predetermined GPS-position data fed into the helicopter. The combined images
were incorporated into a personal computer using Quantum GIS 1.8.0. A total of 55 20-m-diameter circles were randomly scattered over the sandflat and all feeding pits contained in them traced on the display. The measurement error in area for a smallest stingray-pit equivalent was assessed by measuring the area of each of 22 15-cm × 15-cm square marker points (see Appendix 2).

3. Results

3.1. Environmental characteristics and ghost shrimp distribution over the sandflat

The water pressures recorded at the cross-marked point on the sandflat (Fig. 1D) between 17 and 18 August 2012 were converted into the water-column heights by a factor of Δ1 cm in height to Δ1.031 gw cm−2 in pressure under the overlying water with a mean practical-salinity-unit value of 31 for August (A. Tamaki, unpublished data). The highest tides with nearly the same water-column heights (ca. 2.7 m) occurred at 20:23 on Day 1 and 08:11 on Day 2. The diurnal inequality was found for the lowest tides, with the nighttime water-column height of 0.4 m at 02:21 on Day 2 (sunset at 19:02; sunrise at 05:46). Between the daytime lowest-tide times on both dates, the continuous submergence duration in the first tide was 11.3 hours and that in the second tide 10.6 hours.

The surface elevation contours (DEM) of the sandflat did not form a zonation pattern parallel with the upper and lower shorelines but consisted of a mosaic of high and low profiles (Fig. 3A). Around the southeastern part of the sandflat, a large area of the higher surface with > 0.56 m in elevation extended from the uppermost shore seaward pointing toward the westernmost breakwater (Fig. 3B, Area I). Toward the northwestern half of the sandflat, Area I connected with zones of the same elevations on the upper shore, which comprised the wider one (Area II) and the narrower fragmented ones along the uppermost shoreline (Area III). The lower surface with ≤ 0.56 m in elevation occupied a wide seaward zone in the northwestern half of the sandflat (Area IV). At its
northern periphery, a very narrow extension ran counterclockwise to connect with a wider belt at the
same lower elevations between Areas II and III (Area V). On the lowest shore, Area VI and Area VII
lay seaward of Area I and Area IV, respectively; Area VII was outside the 2012 aerial survey domain.

The continual submergence durations between the daytime lowest-tide times on Days 1 and 2 at
points other than the above-mentioned cross-marked point on the sandflat were estimated separately
for the first and second tides and their isopleths over the sandflat drawn (Fig. 3C,D). For this
procedure, (1) using “smooth.spline” function in “R” (R Core Team, 2012), spline interpolation was
made to obtain a complete curve for water-level variation through time at the cross-marked point, in
which the values were standardized to the mean sea level at the nearby tide gauge station (Fig. 1D)
and (2) the submergence duration at any point was estimated by taking into account the difference in
elevation from the cross-marked point on the DEM (Fig. 3A). The color gradation pattern in the
first-tide submergence duration was similar to that in the elevation contour (Fig. 3C), with 11–12.4
hours on the lower shore and 8–10 hours on the uppermost shore. In the second tide, the lower shore
was submerged less than in the first tide by 0.7 hours (Fig. 3D).

The sand-column thicknesses over the sandflat ranged from 9 to 120 cm, with mean ± SD \[N
(number of points) = 137\] being 47.2 ± 19.9 cm (Fig. 3E). The Kriging interpolation found the
thickest columns (around 100 cm) in the northwestern part of Areas II and V and the thinnest
columns (around 30 cm) in Area IV. The latter area was generally encircled with gradually thicker
sand columns outward. The thinnest columns also occupied a substantial part of the uppermost
sandflat.

The numerical densities of \(N.\ harmandi\) (mean ± SD inds. and maximum \(m^2\), \(N\): number of
points) were 103.5 ± 65.2 and 268 (\(N = 120\)) in 2011, 123.3 ± 50.4 and 351 (\(N = 138\)) in 2012, and
134.3 ± 62.6 and 343 (\(N = 39\)) in 2013 (Fig. 3F–H). In 2011 and 2013, the lowest-shrimp-density
area coincided with Area IV, with the lowest elevations and thinnest sand columns (Fig. 3A,E). This
area was generally encircled with gradually higher-density areas outward. The small, highest-density patch occurred in Area V with the thickest sand columns. In 2012, the lowest-shrimp-density area shrunk into three separate patches, while the second lowest-density area expanded especially toward the uppermost shore.

3.2. Dimensions of stingray foraging traces based on manual survey on the sandflat

The ranges for the three dimensions of the stingray foraging traces that were measured manually over the sandflat were: (1) feeding pits \[N (number of samples) = 35\]: 3.4–20.4 cm in maximum depth, 243–8898 cm² in area, and 270–57200 cm³ in volume; and (2) associated sinuous furrows \[N = 17\]: 2.8–6.0 cm in mean depth, 510–52543 cm² in area, and 1140–54600 cm³ in volume. In the feeding pits, maximum depth deepened with area, and the best-fit model between two variables was expressed as a power function, which was nearly of the same form with the upper one of the two previously known functions over an areal range beyond the maximum value in 2012 (Fig. 4A, solid curve and upper broken curve). This indicates that largely in the present manual survey, the newest group of the feeding pits formed within one day was selected (i.e. ones formed during the second high tide). For sinuous furrows, their mean depths varied little, with grand mean ± SD \(N = 124\) being 4.2 ± 1.7 cm (Fig. 4B). The best-fit models between volume and area were expressed as a logistic function for the feeding pit and as a power function for the sinuous furrow (Fig. 4C,D). Since the regression curve for the feeding pit reached an asymptotic value at around the maximum area, the estimation of volume for the areas beyond 1.0 m² would likely to be made with minimal errors.

3.3. Distribution and abundance of stingray foraging traces on the sandflat based on aerial surveys

The measurement error in area for a smallest stingray-pit equivalent was assessed as 0.047 ±
0.004 m² (mean ± SD, number of markers = 24) against 0.04 m² of each marker area. The individual areas of the newly-formed stingray feeding pits that were detected by the aerial survey over the sandflat in 2012 ranged from 243 to 17700 cm², with mean ± SD being 1060 ± 816 cm² (total number of pits = 18103). The area (A, cm²)-frequency distribution was divided into six groups (Fig. 5A, G1–G6): G1 with A ≤ 500 and N (number of pits) = 3159 (17.45% of the total number); G2 with 500 < A ≤ 1000 and N = 7397 (40.86%); G3 with 1000 < A ≤ 2000 and N = 6275 (34.66%); G4 with 2000 < A ≤ 4000 and N = 1066 (5.89%); G5 with 4000 < A ≤ 6000 and N = 136 (0.75%); and G6 with A > 6000 and N = 70 (0.39%). The mean ± SD values in A from G1 to G6 in order were: 383 ± 72, 744 ± 141, 1353 ± 258, 2573 ± 497, 4788 ± 546, and 8383 ± 2250. To give a reference measure, the pits are transformed into circles in shape, with the original areal boundaries and means for these groups converted into the diameter boundaries and means (DB and DM, cm): G1 (DB ≤ 25; DM = 22), G2 (25 < DB ≤ 36; 31), G3 (36 < DB ≤ 50; 41.5), G4 (50 < DB ≤ 71; 57), G5 (71 < DB ≤ 87; 78), and G6 (DB > 87; 103). The minimum, maximum, and grand mean diameters were 17.6, 150.1, and 36.7 cm, respectively. The feeding pits were distributed widely over the sandflat, with the larger ones centered on Area IV (Fig. 6A). The mean ± SD and maximum numerical densities of all feeding pits inclusive were 16.5 ± 8.4 and 59.0 pits per 100 m², respectively (number of 10-m × 10-m grid cells = 1187).

The individual sinuous-furrow areas ranged from 865 to 82059 cm², with mean ± SD being 18475 ± 15988 cm² (total number of furrows = 119), in which 91 furrows were associated with feeding pits (Fig. 5B). Almost all feeding pits accompanying sinuous furrows (96%) were over 2500 cm² in their individual areas (Fig. 5C), which belong to the feeding-pit groups G4–G6 (Fig. 5A). A weak positive correlation was detected between sinuous-furrow and feeding-pit areas (r = 0.26; P < 0.05; Fig. 5D). The sinuous furrows were distributed mainly in Area IV (Fig. 6B; number = 73), in which the mean ± SD and maximum numerical densities were 0.3 ± 1.0 and 13.6 furrows per 100 m².
The mean ± SD numerical densities over the sandflat were 0.1 ± 0.6 100 m² (number of cells = 1187). The 95% kernel home ranges of feeding pits covered most to almost all of the sandflat in all Gns (from G1 to G6 in order: nearly 100, 99, 95, 93, 82, and 69% in area), while a successive ontogenetic change was observed for the 50% kernel home ranges (Fig. 7). The position of the largest area of each Gn shifted gradually from the southeast, through the northwest, to the northeast. The area shrank markedly from G1–G3 (42.2–48.1%) to G4–G6 (19.3–33.6%).

In the GLM fitting to test for the selectivity of stingrays of each size group for prey (ghost shrimp) density and/or sandflat elevation (Table 1; Fig. 8), the highest frequencies of the best-fit model among all runs were recorded for Model 3 in G1, G2, G4, and G6, and for Model 2 in G3. Model 1 was slightly more frequent than Model 3 in G5, and Model 4 was never adopted in all Gns. The smallest stingrays (G1) showed a strong selectivity for areas with higher prey densities over a wide elevation range, while the largest ones (G6) for areas with lower elevations and lower prey densities. An ontogenetic transition was found between these two groups. Although the best-fit models were different between G2 and G3, their overall graphic shapes depicted a similar pattern, with only weak selectivities for higher prey densities largely irrespective of the elevation. A marked shift in the foraging pattern took place at G4, with a strong selectivity for lower elevations over a wide prey-density range. This tendency was followed by G5. This finding raised the question as to whether the larger stingrays (G4–G6) might utilize the lowest sandflat with the higher prey densities (Area VII) than in Area IV (Fig. 3A,B,G), which was unanswerable from the 2012 survey result due to the submergence of Area VII. This was examined by comparing the distribution of feeding pits with ≥ 0.25 m² in area between the 2011 and 2012 aerial surveys (Figs. 5A,C and 9A,B; 2011 data included the older pits); the measurement error in area for a smallest stingray-pit equivalent in 2011 was assessed as 0.0308 ± 0.0055 m² (mean ± SD, number of markers = 22) against 0.0225 m² of...
each marker area. In 2012, the mean ± SD number of these pits per 100 m² over the aerial survey domain was 1.9 ± 1.5 (number of grid cells = 1187). The distribution patterns of those pits in that domain were similar between the two years. In 2011, the mean ± SD numerical densities were significantly higher in Area VII than in Area IV (3.2 ± 1.1 versus 2.3 ± 1.8 100 m⁻² as converted from the densities per 20-m-diameter circle area; \( P < 0.05 \) in Mann-Whitney U-test for medians; number of circles = 11 for both). Thus, the larger stingrays foraged throughout the lower sandflat, within which they might slightly more utilize the sub-area on the lowest zone with higher prey densities.

3.4. Distribution pattern of stingray bioturbation rates over the sandflat

In 2012, the mean ± SD and maximum stingray-excavated-area densities based on those values for the 10-m × 10-m unit grid cells over the 107516-m² sandflat were 194 ± 147 (\( N = 1187 \)) and 1553 cm² m⁻² (Fig. 10A). Applying the regression equations of the individual displaced-sediment volume versus excavated area for the feeding pit and sinuous furrow (Fig. 4C,D) to their excavated-area densities, the mean ± SD and maximum displaced-sediment-volume densities were estimated at 786 ± 560 (\( N = 1187 \)) and 9399 cm³ m⁻² (Fig. 10B). It is estimated that collectively, a total of ca. 86-m³ sediment was displaced over the sandflat in one day. The vulnerability of prey (ghost shrimps) to sediment excavation by stingrays might rather depend on the latter’s feeding-pit depth relative to the sand-column thickness, as the lower portion of the sand column could be a refuge for deep-dwelling infauna. Applying the regression equation of the individual maximum depth versus excavated area for the feeding pit (Fig. 4A) to respective feeding-pit areas in the 2012 aerial survey, the maximum depth was estimated for every feeding pit and its proportional depth to sand-column thickness there (Fig. 3E) calculated and plotted over the sandflat (Fig. 10C–F). The widest area in the higher-proportion groups (> 30%) coincided with Area IV, which had the thinnest
sand columns. In particular, the pits with > 50% proportion mainly existed there, where the lowest
prey-density plots and the two largest pits (G5, G6) were concentrated (Figs. 3F–H and 7E,F).

The spatial variation in stingray excavated-area density and displaced-sediment-volume density
over the sandflat in 2012 was examined for its sub-areas as classified by the combination of sandflat
elevation and prey density that were estimated from the ordinary Kriging interpolations (Fig. 3A,G).

Here, each of the elevation and density ranges was equally divided into three classes (mean ± SD
given in parenthesis): (1) elevation (m): 0.34 ≤ low (0.45 ± 0.09) < 0.61, 0.61 ≤ mid (0.73 ± 0.07) <
0.88, and 0.88 ≤ high (0.94 ± 0.04) ≤ 1.15; and (2) ghost shrimp density (number of inds. m\(^{-2}\)): 28.6
≤ low (89.0 ± 15.8) < 107.82, 107.82 ≤ medium (132.9 ± 20.5) < 187.01, and 187.01 ≤ high (206.0 ±
18.0) ≤ 266.20. During the aerial survey period in 2012, the mean water levels in the low- and
high-elevation sub-areas at the high tides were 2.6 m and 2.1 m, respectively (each equal for the first
and second high tides). Those values at the night lowest tide were 0.3 m and 0 m (= exposed). The
nine possible sub-areas comprised discrete patches of a collection of unit grid cells (Fig. 11A): SA1
(low elevation; low prey density), SA2 (low; medium), SA3 (low; high), SA4 (mid; low), SA5 (mid;
medium), SA6 (mid; high), SA7 (high; low), and SA8 (high; medium); SA9 (high; high) was
non-existent. SA1, SA2, SA4, and SA5 together accounted for 86.9% of the whole sandflat area (Fig.
11B). Based on the sum total area of each SA and on the excavated-area and
displaced-sediment-volume densities for each grid cell (Fig. 10A,B), the sum totals for excavated
area and displaced-sediment volume were estimated for each SA (Fig. 11C,D). The mean densities of
excavated area and of displaced-sediment volume per square meter were used as the
sub-area-specific measures for the degree of stingray bioturbation rates per day. The highest degree
of rates was found for SA1 (276.9 cm\(^2\) m\(^{-2}\) and 1058.9 cm\(^3\) m\(^{-2}\); Fig. 11E,F), while the lowest values
were about half, respectively (126.1 cm\(^2\) m\(^{-2}\) and 537.2 cm\(^3\) m\(^{-2}\) for SA8). The mean ± SD values for
the SA1–6 inclusive (higher group) and SAs 7 and 8 inclusive (lower group; mean only) were 223.0
± 33.0 and 132.1 cm$^2$ m$^{-2}$ in excavated-area density, and 878.6 ± 126.1 and 550.7 cm$^3$ m$^{-2}$ in
displaced-sediment-volume density, respectively. The lower degree of bioturbation rates in the
higher-elevation areas (SA7,8) was due to the absence or very low contributions of G4–G6 and SF
(sinuous furrow). The proportional contribution of G1 increased with prey density in each of SA1–3,
SA4–6, and SA7,8 groups. Through all sub-area groups, the highest contributions were made by the
intermediate feeding-pit-size groups (G2,G3) which were most abundant in the stingray population
(Fig. 5A). For excavated-area density, the ranges in percentage contribution of G1, G2+G3, and
(G4–G6)+SF, with their sub-areas where each edge value was found given in parenthesis, were:
3.3% (SA1)–9.0% (SA8), 48.6% (SA1)–89.3% (SA7), and 5.9% (SA7)–48.1% (SA1), respectively.
Those values for displaced-sediment-volume density were: 5.2% (SA1)–12.5% (SA8), 49.6%
(SA1)–86.3% (SA7), and 7.0% (SA7)–45.2% (SA1), respectively.

4. Discussion

In spite of wide recognition of rays as a prominent epifaunal biodiffusor of estuarine and coastal
soft sediments (Cadée, 2001; Hall et al., 1994; Kristensen et al., 2012), quantitative measurement or
estimation of their sediment excavation rates has been limited. On the Tomioka sandflat, foraging
traces of *D. akajei* became numerous rather abruptly from 1995 (Harada and Tamaki, 2004), which
has prompted us to undertake a proper assessment of their bioturbation rates. It is suspected that the
proliferation of stingray foraging traces on the sandflat might be related to a recent trend in
population increases in some rays and small-bodied sharks occurring in estuarine and coastal waters
over a wide geographic range (Heithaus et al., 2010; Myers et al., 2007). These authors’ view of
meso-predator release following the decline of large-bodied sharks (apex predators) might explain
the opposite fishery landing trends between rays and sharks in Ariake Sound, as summarized in
Yamaguchi (2005). Intertidal sandflats in the estuarine and coastal waters of western Kyushu appear to have entered a new regime characterized by intense stingray excavations during the late spring to mid-autumn months (Harada and Tamaki, 2004; Takeuchi et al., 2013). In particular, north-facing sandflats in the region become subjected to chronic disturbances throughout the year, as they normally receive seasonal wind-induced waves during mid-autumn to mid-spring (Tamaki, 1987).

How foraging sites are selected by predators affects prey population structure and sediment bioturbation (Hall et al., 1994). The prey-density-dependent foraging pattern has been demonstrated for a limited number of species of rays from shallow embayment or lagoon waters. In the subtidal habitats, the predation impact on the local prey population was devastating (Peterson et al., 2001) or modest (Ajemian et al., 2012). To our knowledge, Hines et al. (1997) is the only other study that provides a detailed description of rays’ prey-patch use for tidal-flat habitats. The foraging activity of eagle rays (*Myliobatis tenuicaudatus*) was low and independent of infaunal bivalve prey densities but increased linearly beyond a threshold density, not reaching satiation. This could lead to the leveling off the bivalve density over the survey area as rays preferentially forage in high density patches and thus smooth gradients. This total survey area was 12.5 ha in which both ray feeding-pit and bivalve densities were censused manually for the ca. 1/5 subset areas and extrapolated to the whole. The total area in the present study (11 ha) is nearly equivalent to the above value, with the aerial survey enabling analysis for the entire area. For rays, aerial surveys have been used to map seagrass-meadow fragmentation caused by cow-nose ray foraging over a wide area of the shallow subtidal bottom (Hovel and Lipcius, 2001; Orth, 1975). The present study has also made the elevation contours of the target area in fine resolution, which is relevant to the understanding of spatially varying utilization of tidal flats by high-tide predators incurring the risk of being stranded with receding tides.

Ghost shrimp (Callianassidae) are one of the preferred food items for rays occurring in intertidal
(Harada and Tamaki, 2004; Howard et al., 1977; Tillett et al., 2008) and shallow subtidal (Ajemian and Powers, 2013; Ebert and Cowley, 2003; Gray et al., 1997) sandy beds from wide geographic regions. Furthermore, in intertidal sandflats, ghost shrimp burrows and ray feeding pits co-occur sometimes both in high densities (D’Andrea et al., 2004; Martinell et al., 2001; Myrick and Flessa, 1996; Takeuchi et al., 2013). The larger stingrays can excavate the sediment deeper to obtain the larger ghost shrimps residing in the lower portion of the sand column (Ebert and Cowley, 2003; Tillett et al., 2008). Since ghost shrimps are powerful bioturbators themselves (Flach and Tamaki, 2001; Pillay and Branch, 2011), the ray–ghost shrimp relationship highlights a complex bioturbation system in those sandflats. On the Tomioka sandflat, positive responses by stingrays to ghost shrimp densities were found for the smallest fish-size groups, with the strong one in G1 and weak ones in G2 and G3 (Figs. 7 and 8). There, feeding pit numbers gradually increased with shrimp numbers, with no threshold prey density. As demonstrated for rays detecting the presence of infaunal buried prey (Blonder and Alevizon, 1988; Montgomery and Skipworth, 1997; Tillett et al., 2008; Tilley et al., 2013), stingrays may sense ghost shrimps by means of olfaction, electoreception, and mechanoreception of water flow through shrimp burrow openings. If so, ghost-shrimp burrow opening densities would serve as a cue for stingrays to excavate the sediment. The mean maximum depths for the present six stingray feeding-pit groups, G1 to G6, were 6.5, 8.4, 10.7, 13.9, 17.8, and 22.3 cm, respectively (estimated from Figs. 4A and 5A). As the mean depth of the upper portion of the adult *N. harmandi* burrow (above the node of the Y) is 9.6 cm (Tamaki and Ueno, 1998), the excavation of sediment for ghost shrimps residing below the node in their burrows would be less efficient for stingrays in G1 and G2 than in G3 to G6. Thus, by foraging in the area with higher prey densities, the smallest stingrays could compensate for their inefficient gain per feeding bout. Because of their individual smaller impact on ghost shrimps and medium population density (Fig. 5A), the smallest stingrays’ prey-density-dependent foraging behavior would not have a significant
effect on the leveling off shrimp densities over the sandflat.

High-tide predators on tidal flats must withdraw to deeper waters during ebb tide. For the Atlantic stingray, *Dasyatis americana*, spatial segregation was found within a shallow reef environment, with beaches utilized by the smallest rays, deeper waters (> 10 m) by the largest ones, and both by intermediate-sized ones (Aguiar et al., 2009). On the Tomioka sandflat, the larger stingrays (G4–G6) foraged mainly in the lower shore (Figs. 6–9), suggesting that they are especially cautious about the water-depth-range threshold to position themselves in (≥ 2.6 m at the highest tide). The surface elevation higher by 0.5 m (Fig. 3A) was avoided by the larger stingrays. Thus ghost shrimps in the upper shore escaped from the larger stingrays’ predation (high-intertidal refuge). For a dense population of the ghost shrimp, *Nihonotrypaea japonica*, inhabiting the upper part of an extensive intertidal sandflat in Ariake Sound (Shirakawa sandflat), its recent severe decline, almost to the extermination, is suspected to have been caused by increased predation pressure from *D. akajei* (Takeuchi et al., 2013). In this case, large stingrays invaded as far as the uppermost shoreline bounded by the concrete wall. Using the shore-normal elevation profiles (fig. 1C in Takeuchi et al., 2013) and the temporal change in water level recorded at one point (Yamada et al., 2009) of the sandflat, the highest water depth at the uppermost shore is estimated at 2.54 m. On the lower Tomioka sandflat, ghost shrimps appeared to escape from predation to some extent around the lowermost shoreline (Area VII: Fig. 3B) probably due to the thickest sand columns there (sediment depth refuge), while they were subjected to the strongest predation pressure by the larger stingrays in the more landward part from Area VII (i.e. Area IV) with the thinnest sand columns (Figs. 3E–H, 9, and 10C–F). Although adult ghost shrimps were ingested by the larger stingrays, newly-recruited juveniles appeared to be neglected (A. Tamaki, unpublished data), possibly having brought about an alternate yearly change in shrimp density in Area IV (Fig. 3F–H). The sand-column thickness of the *N. japonica*-inhabited zone of the Shirakawa sandflat (1–2 m; Wardiatno et al., 2003) is much
greater than that of the Tomioka sandflat (Fig. 3E), which might afford a sufficient sediment depth
refuge at the shrimp burrow bottom (70 cm below the surface; Tamaki and Ueno, 1998). However,
underground pore-water oxygen concentrations were more hypoxic on the Shirakawa sandflat (mean
concentrations 30 cm below the exposed sandflat surface, 3.8 mg l$^{-1}$ in Tomioka versus 0.6 mg l$^{-1}$ in
Shirakawa; Wardiatno et al., 2003). As the burrow of *N. japonica* has only a single surface opening,
with more limited water exchange with the overlying water column (Tamaki and Ueno, 1998), the
shrimp would come up nearer to the surface for ventilation.

Behavioral thermoregulation may explain the ontogenetic shift in the utilization of shallow
habitats by some ray species (Matern et al., 2000; Vaudo and Heithaus, 2013). This is unlikely to
occur in stingrays on the Tomioka sandflat, as swift flood currents over short intertidal distances
with a small elevation difference would rapidly mix the entire water mass (Sections 2.1 and 3.1).

Spatially varying foraging behaviors of rays within an intertidal habitat can generate
spatially-structured disturbance on the substrata (Hines et al., 1997). The estimation for the total area
disturbed by predators is confronted with a problem as to how the “total area” under study is
delimited, in which predators’ behavioral information can be used to define their feeding grounds
(Hall et al., 1994). On the Tomioka sandflat, the relatively low degrees of sediment excavation by
the smallest-size group of stingrays (G1: low individual bioturbation rate × medium abundance) and
the largest-size groups (G4–G6: high individual bioturbation rate × low abundance) were spatially
structured, owing to their respective utilization patterns for micro-habitats (Fig. 11). This spatial
heterogeneity was homogenized by the dominant intermediate-size groups in the population (G2 and
G3: medium individual bioturbation rate × high abundance), which appeared to be generalists in
selecting prey patch and sandflat elevation, resulting in both excavated-area and
displaced-sediment-volume densities over the sandflat confined to the small ranges by a factor of
1.6–1.7 (i.e. Sub-areas 1–6 versus 7+8: Fig. 11E,F).
As a first necessary step toward the proper assessment of sediment excavation rates by rays, we examined the numerical, excavated-area, and displaced-sediment-volume densities of newly-formed pits on a daily basis as a basic set of bioturbation rates and compiled published data (Table 2). The papers showing at least two rates are listed in the table, excluding those only with data on excavated-area proportion [e.g. 0.7–1.0% d⁻¹ (Sherman et al., 1983)]. The reworking rate calculated as (displaced-sediment-volume density per day) / (substratum area), which gives a vertical (z-axis) sediment deposition rate on the substratum surface (e.g. D’Andrea et al., 2004), was also not included, since locally displaced sediment is never spread homogeneously over the area. Furthermore, the sediment turnover time, on either areal or volumetric basis, was not included. For one thing, ray populations never regularly excavate sediment of the area one by one in a non-overlapping pattern, often reusing formerly disturbed patches (Cross and Curran, 2004; O’Shea et al., 2012; Fig. 2D–G). For another, reworking of the displaced sediment is done subsequently through complex physical and biological processes in which ghost shrimp bioturbation is partly involved (D’Andrea et al., 2004; Myrick and Flessa, 1996). In most of the previous studies, the three bioturbation rates are not explicitly described. We estimated their (grand) mean values based on ray pits’ diameter, area, depth, and volume, and numerical density given in some of the original texts, tables, and figures, and on our assumptions regarding “new pit” category, pit shape, and time-scale adjustment of rates to daily basis (Table 2; see Appendix 3 for the table footnote descriptions). The present study has achieved the largest total census area (11 ha versus previous 50 m²–2.7 ha), with heterogeneities in prey abundance and topography. The bioturbation rates by the stingray population on the Tomioka sandflat are positioned at relatively high levels.

The present study has demonstrated the effectiveness of a combined aerial and manual survey to provide one reliable way for measuring and estimating ray bioturbation rates in intertidal soft-sediment habitats on a landscape scale. The procedure is applicable to the assessment of
disturbance by any surface-sediment excavators, especially by megafaunal biodiffusors, on tidal flats if their pit dimensions are discernible from the air. The present estimates were obtained based on the stingray’s population structure and ontogenetic change in its heterogeneous micro-habitat utilizations as inferred from foraging trace abundance patterns. The basic premise of the study that feeding-pit size scales with fish size remains to be validated by observing actual fish behaviors. Finally, it must be pointed out that even under favorable weather and sea conditions over an entire spring-tide period enabling consecutive aerial photography, this time frame still poses limitations to the full understanding of the spatiotemporal dynamics of a foraging trace assemblage in tidal flats.

Acknowledgements

The aerial surveys were conducted in accord with the aviation law in Japan and under the permission of the local town office (Reihoku-cho, Kumamoto). We appreciate technical advice from H. Takase for aerial photogrammetry, and S. Shibata and S. Araki for help in processing images on the computer display. We thank Y. Hongo, Y. Saitoh, T. Nakano, S. Sen-ju, N. Takahashi, and A. Tanabe for assistance with field work. Numerous constructive comments and corrections were provided by the two anonymous reviewers. W. Collins kindly corrected the English text. This research was supported by the Environment Research and Technology Development Fund (4D-1104) of the Ministry of the Environment to AT.

Appendix 1. Detailed aerial survey methods and mosaic imaging conducted in 2012

All work below was carried out by Kyushu airlines, Co. (Oita, Japan). Flights were conducted on consecutive calm summer days at a height of 225 m during daytime low tides with nearly the same
water levels on 17 and 18 August 2012, using a manned helicopter equipped with an aerial film
camera (Hiei SE IIα, Osaka Optical Industry, Co., Ltd.). The photo-scale was aimed at 1/1500. Three
straight-line transects were set, with an overlap proportion between adjacent 172.5-m × 172.5-m unit
photographs aimed at 60% (Fig. 1D). Taking into account the possibility of halation from thin
surface waters on the exposed sandflat including those in stingray foraging traces, an excess number
of photographs was taken. They selected 35/65 photographs in Day 1 and 31/68 ones in Day 2 for
later treatment, resulting in 52–85% overlap (mean ± SD = 72.0 ± 4.4%). Aerial-based photography
took approximately 30 minutes to complete the task during the predicted lowest-tide time on each
date (13:45 and 14:21).

To convert the developed film into a digital image, the former was scanned with a resolution of
2540 dpi, using a high-accuracy scanner for photogrammetry (DSW500, LH Systems, Inc.). The
influences of camera-lens radial distortion and film development-associated expansion–contraction
on the developed films were corrected for each unit image (internal orientation), using a stereometric
system software (Stereometric/pro, Siscam S.r.l., Inc.). This software was also used for the
subsequent, external (= relative and absolute) orientations. After image processing, the final ground
resolution was 1.8 cm per pixel in the image, which was sufficient to detect the smallest stingray
foraging traces on the sanflat (see Fig. 2F,G).

In the relative orientation, an optical model for any two adjacent unit images was made, in which
at least six common points (tie points) must be lying in a balanced configuration in their overlapped
part. To fulfill this requirement, in July, 2012, a total of 65 marker points were arranged in and
around the sandflat every ca. 69 m in parallel to aerial transects and ca. 50 m perpendicular to them
(Fig. 1D, red circle points). Each marker point can be identified as the center of a square board or
sheet with 20 or 50 cm in side, painted in a checked pattern with two colors. At each marker point on
the sandflat, a plywood board was secured to a square timber that stood up to 25 cm above the
sandflat surface (see Fig. 2D,E). On the hard substrata surrounding the sandflat, a sheet was attached
to each marker-point plot. As the datum locations for these marker points, three second geographic
datum points established by the Geospatial Information Authority of Japan were available in close
vicinity to the target area, from which one additional datum point was newly installed (Fig. 1D,
white star marks; one datum point is outside the figure). The Cartesian coordinates \((x, y, z)\) of the 65
marker points were determined from the three datum points indicated in Fig. 1D, using an electronic
total station (SOKKIA SET3030R, Topcon, Co.) before and after the aerial survey within a
maximum of 5-hour exposure time on 17 August 2012. In the present study, the elevations were
expressed as the values above the mean sea level at a tide gauge station of the Japan Meteorological
Agency located 6 km south of Tomioka Bay (130°02′E, 32°28′N; Fig. 1B, red star mark); the datum
points’ elevations are described as deviations from the mean sea level of Tokyo Bay. The
coordinate-value errors were assessed by the measurement from two of the datum points toward five
of the marker points (Fig. 1D, denoted by asterisked white stars and red circle points), with their
mean ± SD being 2.86 ± 0.71 cm in longitude, 0.72 ± 0.81 cm in latitude, and 1.74 ± 0.69 cm in
elevation. Sometimes in the laboratory procedure, to achieve a more complete configuration of the
tie points for any two adjacent unit images, conspicuous natural markers were used in addition to
actual markers.

In the absolute orientation, each optical model constructed by the relative orientation was related
to the ground coordinate system based on the above 65 marker points. For this procedure, at least
three of these marker points (control points) must be lying in the overlapped part of any two adjacent
unit images (hereafter termed overlapped-part image). The actual number of control points ranged
from 3 to 10, with mean ± SD of 6.9 ± 1.4.

To attain images that are ortho-projected on a horizontal plane, first, the elevation contours were
drawn at 20-cm height intervals over the sandflat by stereoscopy for every overlapped-part image,
using Stereometric/pro. Tracing points on any one same elevation that were clearly visible on the display automatically generated the corresponding contour line. The steep-slope artificial constructions were treated separately from the sandflat region. The subsequent procedures were conducted using an ortho-image production system software (New Orthomap, Siscam S.r.l., Inc.). Based on the elevation contours, a digital elevation model (DEM) expressed as a triangulated irregular network was constructed for the sandflat (Fig. 3A). All unit images were placed on the DEM. For their ortho-projection, geometric correction (either elongating or shortening of images) was made to correct for potential errors associated with camera inclination and the ground topographic variations. Finally, all ortho-projected unit images were combined into a single mosaic image over the sandflat for each date.

Appendix 2. Detailed aerial survey methods conducted in 2011

The work was carried out by Kaiteki-Kukan, Co., Ltd. (Fukuoka, Japan) and E-System, Co., Ltd. (Hiroshima, Japan), using an unmanned helicopter (72 cm in round-shape diameter and 1.6 kg in weight) equipped with GPS (MK-GPS 1.1, HiSystems GmbH, Co., Ltd.) and digital camera with autofocus function (EOS Kiss X4 with 5184 × 3456 pixels, Canon, Inc.). It took about 2 hours for them to complete the task between 12:30 and 14:30 including the lowest-tide time around 14:20, in which photographed zones were varied with time according to the receding tide. The helicopter automatically flew at a height of 50 m along ten GPS-programmed courses which were roughly in parallel to the three ones used for the 2012 survey. One continual flight was restricted to 16 minutes due to battery capacity. The position of the helicopter was being monitored on a personal computer display. The camera shutter was released with a remote controller for each predetermined position, with overlaps of 30–70% between adjacent ca. 93-m × 62-m unit images of which total number was 34
200. Twenty-two 15-cm × 15-cm square boards had been installed over the sandflat as the marker points.

Appendix 3. Descriptions for footnotes a–j in Table 2

a ND: mean number of pits newly formed per unit seabed area and unit time. EAD: mean of the area excavated by all newly-formed pits per unit seabed area and unit time = mean area excavated by a newly-formed pit × ND. DSVD: mean of the sediment volume displaced by all newly-formed pits per unit seabed area and unit time = mean sediment volume displaced by a newly-formed pit × ND.

b Number of census occasions: 8, each with a 4–6 d set. ND is calculated as a grand mean value for (1/100) × solid-bar values given in reference, fig. 10A. EAD is calculated as a grand mean value for 100 × solid-bar values given in reference, fig. 10C. DSVD is calculated as a grand mean value for 1000 × solid-bar values given in reference, fig. 10D.

c Number of census dates: 3. ND is calculated as a (1/60) × mean for the three values ("new pits") given in reference, table 1. EAD is calculated as a mean for the three values (100 × "percent of the area covered by new pits") given in reference, table 1. DSVD is calculated based on the assumption of half an ellipsoid for pit shape, with EAD and mean newly-formed pit depth (given in reference, text, p. 262: 10 cm).

d ND is calculated from a cumulative pit-diameter-frequency distribution recorded in a 300-m² plot over 7 days (given in reference, fig. 4). EAD is calculated from the same figure based on the assumption of a circle for pit plane shape, with the median in each diameter class used.

e Census time: after each tide; bioturbation rates are converted into those per day by multiplying by 2 due to the semi-diurnal tidal region. Number of census times: 18. ND is assumed to be a 2 × (grand mean value for the 18-tide data); "new pit density" value m⁻² tide⁻¹ given in reference, table 2. Mean
excavated area of a newly-formed pit: 848 cm² (pit ellipse’s mean long and short axes given in reference, text, p. 38). Mean displaced-sediment volume of a newly-formed pit is given as 7400 cm³ by the refilling procedure (reference, text, p. 38).

Mean new-pit diameter: 26.8 cm, estimated from pit-diameter frequency distribution given in reference, fig. 3. Mean excavated area of a newly-formed pit: 565.7 cm², based on the assumption of a circle for pit plane shape. Mean depth of a newly-formed pit: 7.5 cm, based on the half the range value, 5–10 cm, given in reference, text, p. 285. Mean displaced-sediment volume of a newly-formed pit: 2828.3 cm³, based on the assumption of half an ellipsoid for pit shape. ND is calculated as (census area) \times (areal proportion occupied by newly-formed pits given in reference, text, p. 290: 0.0084) / (mean excavated area of a newly-formed pit).

Number of census years: 3. Duration for each year census: 7 days. Daily total census area each year: 1500 m². Total number of detected pits: 108. The areal proportion of these feeding pits in the 1500-m² survey area: 2.42% (given in reference, text, p. 192). The mean individual pit volume: 10064 cm³ (given in reference, text, p. 192).

Number of census dates: 6. Numerical density of pits: mean sum-total number of pits formed in unit census area during the preceding four dates (reference, fig. 4). ND is assumed to be a grand mean value for the six-date data calculated as (numerical density of pits) / (4 \times 707). Mean excavated area and depth of a newly-formed pit: 5000 cm² and 15 cm (reference, text, p. 196). EAD is assumed to be a grand mean value for the six-date data. Mean displaced-sediment volume of a newly-formed pit is assumed to be the volume of half an ellipsoid with the above mean excavated area and depth values, being 50000 cm³. DSVD is assumed to be a grand mean value for the six-date data. The mean values of ND, EAD, and DSVD for the feeding pits corresponding to the prey densities < threshold value (to elicit the predator’s non-linear response) are estimated at 0.0029 m⁻² d⁻¹, 14.3 cm² m⁻² d⁻¹, and 143.5 cm³ m⁻² d⁻¹, respectively. Those values corresponding to the prey...
densities ≥ threshold value are 0.0083 m⁻² d⁻¹, 41.6 cm² m⁻² d⁻¹, and 416.0 cm³ m⁻² d⁻¹, respectively.

ND (21 pits per 762 m² [= (724 + 800) / 2]) and mean diameter (80 cm) and depth (12 cm) for newly-formed pits are given in reference, text, p. 247. Individual mean pit area and mean pit volume are calculated based on the assumption of a circle and half a sphere for pit shapes, respectively.

Based on Fig. 11. For ND, only pits are included (i.e. sinuous furrows are excluded), but for EAD and DSVD, both pits and sinuous furrows are included. The grand mean value for each sub-area group inclusive is given.

References


Quantum GIS Development Team, 2012. Quantum GIS geographic information system.


Figure captions

Fig. 1. Study site. A–D: Intertidal sandflat facing Tomioka Bay (Tomioka sandflat) on the northwestern corner of Amakusa-Shimoshima Island in western Kyushu, Japan. B, red star: tide gauge station of the Japan Meteorological Agency located 6 km south of Tomioka Bay. D, white-colored area: aerial survey domain in 2012 (107516 m² in exposed area). That survey domain in 2011 was extended 20–60 m seaward to the level of the mean low water at spring tides (blue line). Stingray foraging traces were invisible in a narrow strip covered with green algae (Ulva pertusa) along the uppermost shoreline. The cross mark: point installed with water-pressure gauge. The red filled circles: marker points for the 2012 aerial survey. The white stars: datum points for determining the coordinates of these marker points. The asterisked circles and stars: points used for assessing coordinate-value errors. The flight in 2012 was conducted along the three dotted lines, with a unit photographed areal coverage exemplified as the red dotted square.

Fig. 2. Stingray foraging traces. Foraging trace images on the exposed Tomioka sandflat in 2012, taken on the ground (A,B) and from the air (C–G). A,B: Fragments of green algae trapped in some traces. Black spots seen on the sandflat surface are openings of ghost shrimp burrows. C: Close-up view of feeding pits (FP) and sinuous furrows (SF). D,E and F,G: Identical plots taken on 17 and 18 August, respectively. One 20-cm × 20-cm marker point is indicated by the arrows in D and E. The darker parts stand for foraging traces of varying ages, with the newly-formed feeding pits and sinuous furrows indicated red and blue, respectively, in E and G. The two feeding pits with black and red arrows in each of F and G indicate their degradation with infilled sediment in one day.

Fig. 3. Sandflat feature and ghost shrimp distribution maps. Environmental characteristics (A–E)
and ghost shrimp density (F–H) over the Tomioka sandflat. In all panels, the outline of the 2012 aerial survey domain is indicated (Fig. 1D). A: Elevation profile by the ordinary Kriging interpolation based on 2-m mesh Digital Elevation Model (DEM), with values given as heights from the mean sea level at the tide gauge station (Fig. 1B). B: Division of the sandflat into sub-areas with regard to a boundary elevation of 0.56 m (A) and position; Area VII was exposed only in the 2011 aerial survey. C,D: Estimated isopleths of submergence duration in the first and second tides during 17 to 18 August 2012, based on the water-level record at the cross-marked point (Fig. 1D) and elevation profile (A). E: Sand-column thickness distribution by the ordinary Kriging interpolation based on measurements at dot points. F,G,H: *Nihonotrypaea harmandi* numerical density distributions by the ordinary Kriging interpolation based on burrow-opening counts at dot points in 2011, 2012, and 2013, respectively.

Fig. 4. Scatter plots for relationships among three dimensions of stingray foraging traces on the Tomioka sandflat. A: Maximum-depth (cm) and area (m²) for newly-formed feeding pits, with the solid regression curve \[ \text{Depth} = 0.6 \times (10^4 \text{Area})^{0.4} \] from the 2012 survey and with the upper and lower broken regression curves from a previous survey result (A. Tamaki, unpublished data; equations given in Section 2.5, text; \( N \), number of pits); the appropriateness of judgment for the “newly formed” in 2012 was confirmed by the maximum-depth ranges for the newly-formed pits as identified from the manual survey over two consecutive dates in the previous survey. B: Depth (cm) and area (m²) for sinuous furrows associated with newly-formed feeding pits, with 1–19 measurement plots varying with individual furrow sizes (different symbols for furrow identities) and the grand mean depth of 4.2 cm (dotted line). C: Infilled sediment volume (cm³) and area (m²) for the feeding pits (A), with the regression curve given as \( \text{Volume} = 50011.3 / (1 + 28.4 \exp(-8.5 \text{Area})) \). D: Infilled sediment volume (cm³) and area (m²) for the sinuous furrows (B), with the regression
curve given as $Volume = 34.2 \times (10^4 Area)^{0.7}$.

Fig. 5. Stingray foraging trace areal frequency distributions and scatter plots. A–C: Area-frequency distributions of newly-formed foraging traces over the Tomioka sandflat ($N$: number of traces), as obtained from the 2012 aerial survey. A: Feeding pits, with a unit-area class of 0.05 m$^2$ and the subdivision into six groups (G1–G6; see text for their boundary values and number of pits for each group). B: All sinuous furrows, with a unit area-class of 0.2 m$^2$. C: Feeding pits accompanied by sinuous furrows, with those $\geq 0.25$ m$^2$ in area demarcated for analysis of data in Fig. 9. D: Relationship between feeding-pit-associated sinuous-furrow area and feeding-pit area, with respective paired data extracted from B and C.

Fig. 6. Distribution of newly-formed stingray foraging traces by size. A: feeding pits. B: sinuous furrows. $N$: number of traces detected in the 2012 aerial survey domain on the Tomioka sandflat. Each trace is placed at the $(x, y)$-coordinate of its center position and expressed by a semi-transparent circle in proportion to each area.

Fig. 7. Kernel home ranges (95% and 50%) of newly-formed stingray feeding pits by their size groups. A–F: G1–G6 (defined in Fig. 5A) in the 2012 aerial survey domain of the Tomioka sandflat.

Fig. 8. Generalized linear model (GLM) fitting. Graphic representations of the result of fitting to test for the selectivity of stingrays of respective size groups [G1–G6 (Fig. 5A) arranged in columns] for prey (ghost shrimp) density and/or topographic elevation on the Tomioka sandflat. See Table 1 for parameter values in the best fit. The explanatory variables used are given in the four models arranged in rows: prey density alone (Model 1), sandflat elevation alone (Model 2), and both prey
density and elevation (Model 3); Model 4 (null model: indifferent to both prey density and elevation) was never adopted in all Gns and are not shown. The percentage values in the three panels for each of Gns indicate their adoption rates as best fit in each 99 runs. The best-fit case based on AIC is displayed for each model.

**Fig. 9.** Distribution of the larger stingray feeding pits. **A:** For those pits newly-formed with $\geq 0.25$ m$^2$ in area (Fig. 5C: G4–G6) over the 2012 aerial survey domain of the Tomioka sandflat. The density classes divided by Natural Breaks (Jenks) mode are assigned to each 10-m $\times$ 10-m unit grid cell. **B:** For those pits of all ages inclusive at 55 randomly-generated 20-m diameter circles (center positions indicated by cross marks) over the 2011 aerial survey domain, with Areas IV and VII (Fig. 3B) highlighted. For comparison with the densities in 2012, the number of pits contained in each census circle was converted into the value per 100 m$^2$ and expressed by a gray circle area.

**Fig. 10.** Distribution of stingray bioturbation rates and depth over the Tomioka sandflat. **A:** Distribution of the excavated-area density of all newly-formed stingray foraging traces inclusive for each 10-m $\times$ 10-m grid cell over the 2012 aerial survey domain of the sandflat. The densities of traces were divided into classes by Quantile mode. **B:** Distribution of the displaced-sediment-volume density of these traces over the sandflat, as estimated based on each trace’s area (Fig. 6A,B) and the regression equation of volume versus area for the traces obtained by the *in situ* survey (Fig. 4C,D). The densities of traces were divided into classes as in **A. C–F:** Distribution of the percentage proportion of maximum depth (PPMD) of each newly-formed feeding pit in the sand column of the corresponding point over the sandflat; the PPMDs are divided into four classes. Each value is expressed by a semi-transparent gray circle area. The maximum depth for each pit was estimated based on its area (Fig. 6A) and the regression equation of maximum depth versus area for the pits.
obtained by the *in situ* survey (Fig. 4A). The target area of the sandflat was limited to that for the sand-column thickness survey (Fig. 3E).

**Fig. 11.** Division of the Tomioka sandflat by stingray bioturbation rates. **A:** Division into eight sub-areas based on elevation and ghost shrimp density at each 10-m × 10-m grid cell. The whole area was determined according to the overlapped part among the aerial, elevation, and ghost-shrimp density surveys conducted in 2012 (Figs. 1D, 3A,G). White parts: no complete data set available. See text for the boundary values for the low, mid/medium, and high categories in elevation and ghost shrimp density. **B:** Sum total area for each sub-area. **C:** Sum total of the excavated areas of stingray foraging traces for each sub-area, with contributions of respective foraging-trace groups stacked (G1–G6, feeding pits and SF, sinuous furrow). **D:** Sum total of the estimated displaced-sediment volumes of foraging traces for each sub-area. **E:** Excavated-area density of foraging traces for each sub-area. **F:** Estimated displaced-sediment-volume density of foraging traces for each sub-area.
Fig. 1 (Takeuchi and Tamaki, revised)
Fig. 2 (Takeuchi and Tamaki, revised)
Fig. 3 (Takeuchi and Tamaki, revised)
Fig. 4 (Takeuchi and Tamaki, revised)
Fig. 5 (Takeuchi and Tamaki, revised)
Fig. 6 (Takeuchi and Tamaki, revised)
Fig. 7 (Takeuchi and Tamaki, revised)
Fig. 8 (Takeuchi and Tamaki, revised)
Fig. 9 (Takeuchi and Tamaki, revised)
Table 1. Generalized linear model (GLM) fitting to test for selectivity of stingrays of each size group (G1–G6) for prey (ghost shrimp) density and/or topographic elevation on the Tomioka sandflat. See Fig. 8 for graphic displays. Four models were fit to the binary response variable (1 for the observed points on the sandflat; 0 for the randomly generated points), with prey density alone (Model 1), sandflat elevation alone (Model 2), both (Model 3), and null (= indifferent to both; Model 4) used as explanatory variables, assuming a binomial probability distribution for each. The percentage values in the adoption-rate column for each of Gns indicate the occurrence rates as best fit of the 99 runs. For each model, the parameter values in the best-fit linear prediction based on AIC are listed.

<table>
<thead>
<tr>
<th>Feeding-pit group</th>
<th>Model</th>
<th>Explanatory variable</th>
<th>Linear prediction</th>
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<td>Elevation</td>
<td>Intercept</td>
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Table 2. Bioturbation rates about numerical density (ND, numbers m$^{-2}$ d$^{-1}$), excavated-area density (EAD, cm$^{2}$ m$^{-2}$ d$^{-1}$), and displaced-sediment-volume density (DSVD, cm$^{3}$ m$^{-2}$ d$^{-1}$) for newly-formed pits of rays in estuarine and coastal soft-sediment habitats (all sandflats) from different geographic regions.

<table>
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<tr>
<th>Location in geographic region</th>
<th>Intertidal/Subtidal (water depth)</th>
<th>Total census area (number × unit area) (m$^{2}$)</th>
<th>Target rays</th>
<th>ND$^a$</th>
<th>EAD$^a$</th>
<th>DSVD$^a$</th>
<th>Reference</th>
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<td>300 (3 × 100)</td>
<td>stingray</td>
<td>0.026</td>
<td>57.0</td>
<td>145.0</td>
<td>D’Andrea et al. (2004)$^b$</td>
</tr>
<tr>
<td>Florida gulf coast, U.S.A.</td>
<td>subtidal (2–3 m)</td>
<td>60</td>
<td>stingray</td>
<td>0.117</td>
<td>91.0</td>
<td>611.1</td>
<td>Reidenauer and Thistle (1981)$^c$</td>
</tr>
<tr>
<td>same as above</td>
<td>subtidal (NA)</td>
<td>300 (3 × 100)</td>
<td>stingrays</td>
<td>0.082</td>
<td>130.6</td>
<td>NA</td>
<td>Valentine et al. (1994)$^c$</td>
</tr>
<tr>
<td>innermost Gulf of California, Mexico</td>
<td>intertidal</td>
<td>200–600</td>
<td>bat ray and stingray</td>
<td>0.390</td>
<td>330.5</td>
<td>2883.3</td>
<td>Myrick and Flessa (1996)$^c$</td>
</tr>
<tr>
<td>off La Jolla, California, U.S.A.</td>
<td>subtidal (17 m)</td>
<td>50</td>
<td>bat ray and stingray</td>
<td>0.148</td>
<td>84.0</td>
<td>420.0</td>
<td>VanBlaricom (1982)$^f$</td>
</tr>
<tr>
<td>Ningaloo Reef, Western Australia</td>
<td>intertidal</td>
<td>1500 (15 × 100)</td>
<td>stingrays</td>
<td>0.003</td>
<td>11.5</td>
<td>34.5</td>
<td>O’Shea et al. (2012)$^i$</td>
</tr>
<tr>
<td>Manukau Harbour, New Zealand</td>
<td>intertidal</td>
<td>26866 (38 × 707)</td>
<td>eagle ray</td>
<td>0.004</td>
<td>18.1</td>
<td>180.8</td>
<td>Hines et al. (1997)$^i$</td>
</tr>
<tr>
<td>same as above</td>
<td>intertidal</td>
<td>724–800</td>
<td>eagle ray</td>
<td>0.028</td>
<td>138.5</td>
<td>1108.2</td>
<td>Thrush et al. (1991)$^i$</td>
</tr>
<tr>
<td>Amakusa, Kyushu, Japan</td>
<td>intertidal</td>
<td>107516</td>
<td>stingray</td>
<td>0.171</td>
<td>223.0</td>
<td>878.6</td>
<td>this study (sub-areas 1–6)$^i$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.141</td>
<td>132.1</td>
<td>550.7</td>
<td>this study (sub-areas 7+8)$^i$</td>
</tr>
</tbody>
</table>

a–j: see Appendix 3 for descriptions of footnotes.