Habitat use of the East Asian finless porpoise in the northern Aki Nada of the western Seto Inland Sea, Japan

Manuel Eduardo L. de la Paz[1,2], Hajime Sato[1], Takumi Oyama[1], Angelo C. Macario[1,3], Sadaharu Iwasaki[4] and Yoichi Sakai[1]

Contact email: makoy28_delapaz@yahoo.com

ABSTRACT

The East Asian finless porpoise is a small cetacean found in shallow coastal habitats in Asian waters, including those around Japan. While it has been designated an endangered species, recent reports have shown possible subpopulation recoveries, including in the Seto Inland Sea. To update the field data on its occurrence patterns in the northern Aki Nada region, we conducted boat surveys from April 2022 to December 2023 using drones to document habitat use, group composition and behaviour. Our surveys resulted in 0.02 ± 0.03 sightings per km (n = 52) and an estimated density (individuals per km) of 0.08 ± 0.11 porpoises per km (n = 52). Finless porpoises occurred throughout the survey period, except in July and August 2022. The average group size was 2.75 ± 2.53 individuals (range = 1–21), one of the highest records for this species in Japan. Most subgroup sightings were made of pairs (37.1%, n = 63/170), mostly mother-calf pairs. These pairs were mainly observed from February to July and September to November. The GAM analysis resulted in identifying the model with substrate, depth, distance from shore, and sea surface temperature as factors having significant influences on porpoise presence and absence, while location, substrate, depth, distance from shore, and sea surface temperature were identified as factors having significant influences on porpoise group size. The considerably high occurrence of calves suggests that northern Aki Nada is an important breeding, calving, and nursing area for finless porpoises.

KEYWORDS: SEASONAL DISTRIBUTION, MATING PATTERNS, GROUP COMPOSITION, MARINE MAMMALS, COASTAL ENVIRONMENTS

INTRODUCTION

Extensive alterations in marine and coastal habitats caused by anthropogenic development in recent decades have negatively impacted many marine mammal populations, especially small cetaceans that live close to human communities. The East Asian finless porpoise (*Neophocaena asiaorientalis sunameri*), currently identified as the marine subspecies of the narrow-ridged finless porpoise (*Neophocaena asiaorientalis*), is a small-sized cetacean that lives in inshore, coastal environments in northern China, the Korean Peninsula, Taiwan, and Japan. Its freshwater counterpart subspecies, the Yangtze River porpoise (*N.a. asiaorientalis*), lives exclusively in the Yangtze River and its adjoining lakes in China, and has largely been the basis for its assessment as an endangered species (Wang & Reeves, 2017). Both subspecies of *N. asiaorientalis* are threatened by their vulnerability to fishing gear

[1] Graduate School of Integrated Sciences for Life, Hiroshima University, Kagamiyama 1-4-4, Higashi Hiroshima, Hiroshima 739-8528, Japan
[2] Natural Sciences Department, College of Arts and Sciences, University of St. La Salle, Bacolod City 6100, Philippines
[3] College of Fisheries and Marine Sciences, Zamboanga State College of Marine Sciences and Technology, Zamboanga City 7000, Philippines
[4] Takehara Fisheries Research Station, Hiroshima University, Takehara, Hiroshima 725-0024, Japan

entanglement, pollution, boat strikes, population fragmentation, and habitat degradation (Jefferson *et al*., 2009; Kasuya, 2017; Wang & Reeves, 2017; Huang *et al*., 2020; Zuo *et al*., 2023).

Along Japan's coasts, at least five distinct subpopulations of the finless porpoise *N.a. sunameri* have been identified based on geographical, morphological and genetic differences. These subpopulations are found in Ariake Sound and Tachibana Bay, Omura Bay, the Seto Inland Sea, Ise and Mikawa Bays, and Tokyo Bay to Sendai Bay (Kasuya, 2017; Yoshida, 2002; Yoshida *et al*., 1995, 2001). The Seto Inland Sea is the largest habitat and hosts the highest abundance of finless porpoises in Japan (Kasuya, 2017). First surveyed from April 1976 to October 1978 by Kasuya and Kureha (1979) using ferryboats, abundance estimates in the Seto Inland Sea initially ranged between 4,900 and 6,000 individuals, and sighting rates averaged 5.78 porpoises per trip.

Significant declines in the density of the finless porpoise in the Seto Inland Sea were reported by two separate studies conducted 22 years after initial surveys. Kasuya *et al*. (2002) repeated the ferryboat surveys along the same routes as Kasuya and Kureha (1979) and found a remarkable decline in finless porpoise density, especially in the central and eastern side of the Seto Inland Sea, reporting only an average of only 0.30 porpoises per trip. In the same year, Shirakihara *et al*. (2007) conducted aerial surveys in the Seto Inland Sea using a high-wing Cessna at an altitude of 150 m, resulting in a density of only 0.506 individuals/km², the lowest density of the finless porpoise for Japan.

Both Kasuya *et al*. (2002) and Shirakihara *et al*. (2007) noted the drastic disappearance of finless porpoises in the Aki Nada region of the central Seto Inland Sea, which includes an area designated as a national monument for the finless porpoise near Abashima Island, in Takehara City, Hiroshima (Hoyt, 2005). In the 22 years since the finless porpoises in the Seto Inland Sea were first surveyed by Kasuya and Kureha (1979), various human activities, including sand extraction, land reclamation, and the construction of bridges connecting the islands of Honshu and Shikoku, may have played a role in its eventual disappearance or migration from this area (Kasuya, 2017; Shirakihara *et al*., 2007).

The findings of both studies are indicative of trends observed in other finless porpoise populations in East and Southeast Asia (Hashimoto *et al*., 2015; Jefferson & Moore, 2020; Mei *et al*., 2014; Park *et al*., 2012; Park *et al*., 2015; Wang *et al*., 2013; Wang, 2009; Zhao *et al*., 2008), as well as many small-sized cetacean populations living in coastal, freshwater, and marine habitats around the world that have been affected by human interference in their habitats (IWC, 2006). Recent reports of finless porpoise sightings in the mid-western Seto Inland Sea have raised the possibility of their return to the waters of Aki Nada (Chugoku Shimbun, 2012). To ensure the survival of the finless porpoise in Japan, new and updated information about their current ecological status is required (Shirakihara *et al*., 2007; Kasuya, 2017).

To document the current occupancy conditions of the finless porpoise populations in the Aki Nada waters of the western Seto Inland Sea, we conducted boat surveys with the aid of unmanned aerial vehicles (drones) from April 2022 to December 2023. This study documents the presence of the finless porpoise in Aki Nada waters, and assesses their habitat use, seasonal appearance patterns and population compositions, focusing on the potential relationship with environmental variables.

METHODS

Study site

Northern Aki Nada is a semi-enclosed portion of the Aki Nada Basin of the western Seto Inland Sea of Japan (34°21'–34°12'N, 132°39'–133°0'E) and biogeographically positioned as a temperate-water area for marine animals (Nakabo, 2002). Northern Aki Nada is bordered by the coasts of Takehara City (Zones I and IX), Higashi-Hiroshima City (Zone III), Kure City (Zones IV and V) and Osaki-Kamijima Town (Zones I, II, III, V, VI, and VII) of Hiroshima Prefecture, and Omishima of Imabari City of Ehime Prefecture (Zones VII, VIII and IX) (Fig. 1). The western Geiyo Islands (Shimo-Kamagarijima, Kami-Kamagarijima, Toyoshima, Mikado, Osaki-Shimojima, Okamurajima, Koogejima, Ogejima and Kashiwajima Islands) border the northwest and southern part of the study site, while the western coast of Omishima Island borders to the East. In the middle of the study area lies Osaki-Kamijima Island and other smaller associated islands (Fig. 1A). Southwest of the western Geiyo Islands Group opens to the southern part of Aki Nada which connects to Hiroshima Bay to the west, the Iyo Nada Basin to the southwest, and the Mihara Strait and the Hiuchi Nada Basin to the east (Fig. 1A).

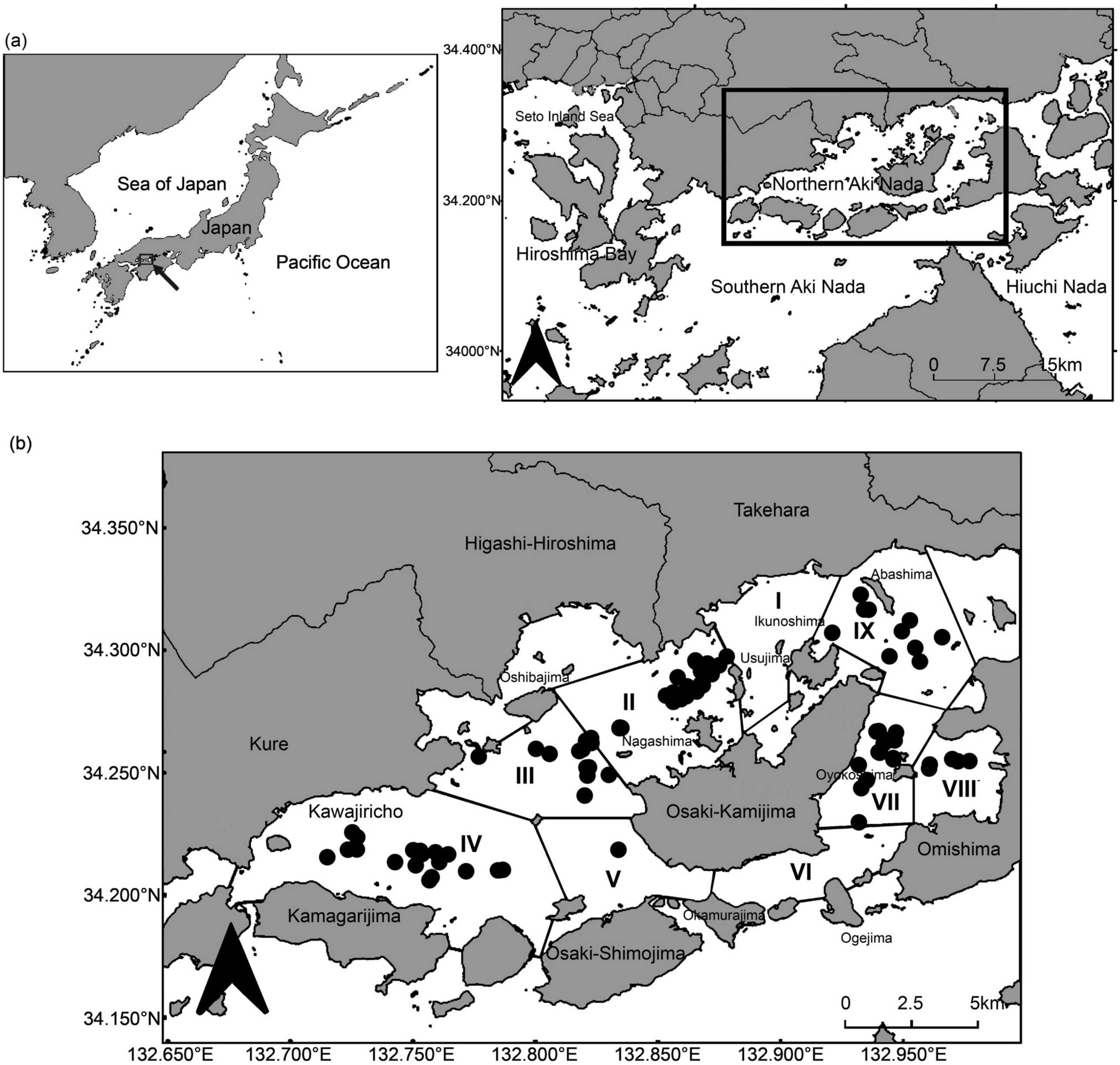

Figure 1. Maps showing the study area of the East Asian finless porpoise. (A) Northern Aki Nada and its location in the western part of the Seto Inland Sea, Japan. (B) Zoned map of northern Aki Nada and its associated islands showing nine survey zones. Block dots represent sighting locations of finless porpoises from April 2022 to December 2023.

The average water depth in northern Aki Nada is 39.9 m (International EMECS Centre, 2008). Because of the semi-enclosed nature of northern Aki Nada, it is protected from strong winds coming from the southern region for most of the year. Beaufort Sea State usually ranged between 0–2 during the surveys, except from December to February, when the western wind affected the western part of the study site. On the other hand, southern Aki Nada usually experienced stronger winds and rougher sea conditions during most of the year, hence limiting our ability to survey those areas.

Data collection

Boat-based surveys for finless porpoises were conducted in the study area at least twice a month (every two weeks) from April 2022 to December 2023, using a 7.71 m, 2.2 t boat *Calanus Maru* of Takehara Fisheries Research Station, Hiroshima University (Takehara City, Hiroshima). No surveys were conducted in August 2023 due to the unavailability of the boat. On 2–4 October 2022, surveys were conducted by the 40.1 m, 400 t research and training vessel *Toyoshio Maru* of Hiroshima University. A total of 256.69 hours of boat surveys during 52 days from May 2022 to December 2023, covering a distance of 2,901.81 km were conducted, 226.56 hours of which were spent on effort, while 30.13 hours were spent observing and attempting to document the behavior of the East Asian finless porpoise.

The study site was divided into nine zones, and each survey zone was assigned one waypoint for the purpose of data collection (Fig. 1B). These waypoints were chosen based on a preliminary survey and previous reports of finless porpoise sightings as well as covering their likely preferred habitats (Kasuya *et al*., 2002). Boat surveys started from Takehara Fisheries Research Station (north side of Zone I, Fig. 1B) and followed pre-determined routes toward the nine waypoints spread across the study area, cruising at an average speed of 16–21 kph. Surveys started at 0900h and finished at around 1500h. The survey usually followed a unidirectional counter-clockwise route around Osaki-Kamijima Island, so as not to pass the same area twice a day. During survey cruises, two to four observers scanned the horizon for signs of surfacing finless porpoises while alternating the use of binoculars and their naked eyes. Once a waypoint was reached, the boat was stopped to allow the researchers to spend 10 minutes scanning the surface for finless porpoises, after which environmental parameters (salinity, sea surface temperature, and dissolved oxygen) were sampled using a hydrometer (Angeltest, Hipo, Taiwan) and a DO meter (OM-51, Horiba, Japan). Often, one or two drones (Air 2S, DJI, China) with built-in cameras were launched to scan the area from an aerial perspective. Sea surface temperature during our study averaged 14.23 ± 2.23°C (mean ± SD) (n = 171) in spring (March to May), 22.14 ± 2.55°C (n = 303) in summer (June to August), 23.81 ± 2.67°C (n = 282) in autumn (September to November) and 13.76 ± 3.35°C (n = 198) in winter (December to February) (Fig. S1A), while dissolved oxygen averaged 8.44 ± 0.94 mg/L (n = 171) in spring, 8.49 ± 0.83mg/L (n = 303) in summer, 7.34 ± 0.81mg/L (n = 282) in autumn and 8.64 ± 1.44 mg/L (n = 198) in winter (Fig. S1b).

If an individual or group of finless porpoises were spotted by any of the observers or drone pilot on effort, the boat was stopped and the location of the sighting was recorded using a handheld global positioning system (GPS) (eTrex 22, Garmin, USA) or the drone's internal GPS. The depth of the sighting location was determined using the boat's navigational system with sonar (RF-8400NFD, Royal's Navigational Systems, Japan). Drones were launched to observe and video-record the behaviour, group size, and composition of the finless porpoise from the air at an altitude of 20–120 m. The drone would follow the animals for as long as possible, or as long as drone batteries for the drone could permit (15–20 minutes for each flight). Finless porpoises often took long dives which made tracking them difficult. During the group follows, observers on the boat were asked to make their best estimate of the porpoises' group size (Mann, 1999). The estimation would then be checked after watching the videos recorded by the drone. Group follows ended when all of the drone's batteries ran out (5–7 batteries) or if no more porpoises were seen at the surface. After the interaction ended, the search effort would resume until all survey points were covered.

The average search effort was 4.36 ± 1.37h (n = 52) and the average distance covered was 58.04 ± 18.44 km (n = 52) per survey day (Table S1). There was no difference in the search effort in terms of time across the four survey seasons (see below) (Kruskal-Wallis test, H = 2.98, p = 0.4).

Data analysis

Sightings of finless porpoises across the study area were plotted on a map using QGIS Software Version 3.43.3 (QGIS Development Team, 2023). Sightings were organised and logged with environmental and geographical data. Location coordinates obtained from a hand-held GPS and the drone's internal GPS were measured with their corresponding distances from the nearest coastline, and substrate data was derived from bathymetric maps issued by the Japan Coast Guard (Bathymateic Map No. 6386, 1987).

The occupation rate of the finless porpoise among the nine zones within northern Aki Nada was analysed by a coefficient of area use (Karczmarski *et al*., 2000), which ranges between 0.0–1.0, where sightings were assigned according to which zones they were located, and the number of sightings was divided by the number of times the surveys covered a zone.

Sighting rates were computed as the total number of sightings per distance covered in each survey day, while porpoise density was computed as the estimated total number of individual porpoises per distance covered in each survey day. Sightings often involved one or more subgroups. To properly distinguish a group from a subgroup, we defined a group, which was usually synonymous with a sighting, as all the porpoises sighted within an area of approximately 100 m radius from a focal animal/group (Irvine *et al*., 1981). On the other hand, subgroups were smaller groups within a sighting and composed of porpoises associated within 10 m from any other member of the group (10 m 'chain rule'; Shane, 1990; Smolker *et al*., 1992). Group and subgroup numbers were counted and estimated from drone videos.

Mother and calf pairs were not distinguished as a separate subgroup if they were associated with another adult/male or group of males attempting to mate (see below) but were considered separate if they were sighted alone or outside the 100 m radius of another individual or group. Calves were distinguished from adults based on size, as being half to three-quarters of an adult, and always swimming close to an adult, often suckling (Christie *et al*., 2022). These were confirmed by reviewing the video recordings taken by the drone. Because individual porpoises were difficult to identify due to the lack of distinguishing marks on their bodies visible from a drone, videos were reviewed repeatedly and carefully to avoid double counting as much as possible, to obtain a minimum group size estimate, especially with the tendency of porpoises to dive and resurface unpredictably. However, this is still not a complete assurance that porpoises could not be double counted in one day, especially during days with multiple sightings.

Statistical analysis

Data of sightings per km, the estimated total number of porpoises per km, total subgroups per km, and calves per km for each survey were grouped into oceanographic seasons and compared using one-way ANOVA and Kruskal-Wallis rank sum tests, depending on the homogeneity of variance of the data. Oceanographic seasons were grouped into four periods from April 2022 to December 2023. It was grouped into two categories: high and low-water temperature, depending on the rise and fall of sea surface temperature. Based on our field measurements, sea surface temperature started to rise from April until it peaked in September and began to fall from October until March (Fig. S1).

Generalised Additive Modeling (GAM; see Guisan & Zimmermann, 2000; Hastie & Tibshirani, 2017) was applied to see if the presence/absence of porpoises, the estimated number of porpoises per subgroup (group size), the presence/absence of calves, and the number of calves encountered were influenced by environmental variables such as location, sea surface temperature, salinity, depth, dissolved oxygen, distance from shore, substrate type and oceanographic season. In this context, 'absence' of porpoises and calves referred to zones visited with no sightings of finless porpoises (and calves), while 'presence' meant otherwise. Hence, we treated the presence/absence of porpoises and calves as categorical data which merited the use of the binomial family with a logit function. In contrast, the estimated number of porpoises and number of calves were analysed as continuous numerical data using the negative binomial family, because the model with the Poisson distribution showed overdispersion and did not fit the model well. The smoothing function was applied to continuous variables, such as temperature, depth, distance from shore, and dissolved oxygen to identify non-linear relationships, while location, substrate, and oceanographic season were treated as categorical independent variables. The best-fit model was selected using the 'dredge' function in the R package of MuMln by choosing the model with the least Akaike Information Criterion (AIC) (Bartoń, 2022). A log-likelihood ratio test of deviances assuming a χ^2 distribution was performed to compare the final and null models. These analyses were conducted in R software version 4.0.2 (R Core Team, 2021) using the mgcv package.

RESULTS

Distribution pattern

We detected the East Asian finless porpoise, the only cetacean species encountered throughout these surveys, 52 times in 26 of the 52 days (50%) of surveys. There were 0.02 ± 0.03 sightings per km (n = 52) and an estimated density (individuals per km) of 0.08 ± 0.11 porpoises per km (n = 52). Finless porpoises were present during all the months of our study period, except August and September 2022 (Fig. 2). The sighting rate of the finless porpoise was 0.98 ± 1.28 times per day (n = 52). There was a significant difference in the sightings per km among the oceanographic seasons (One-way ANOVA, $F(3, 49) = 2.88$, $p = 0.005$) as sightings were higher between April and September 2023 (Tukey's pairwise post-hoc test, $p < 0.05$; Table 1). The density of porpoises (individuals per

Table 1

Occurrence patterns of the East Asian finless porpoise in northern Aki Nada of the western Seto Inland Sea, Japan, for every oceanographic season.

	Sighting rate (sightings per km)	Individual density (porpoises per km)
April–September 2022	0.01 ± 0.02 (14)	0.06 ± 0.09 (14)
October 2022–March 2023	0.01 ± 0.03 (18)	0.05 ± 0.10 (18)
April–September 2023	0.04 ± 0.04 (15)	0.15 ± 0.12 (15)
October–December 2023	0.02 ± 0.03 (5)	0.09 ± 0.10 (5)

Mean ± SD values are shown with n in parentheses

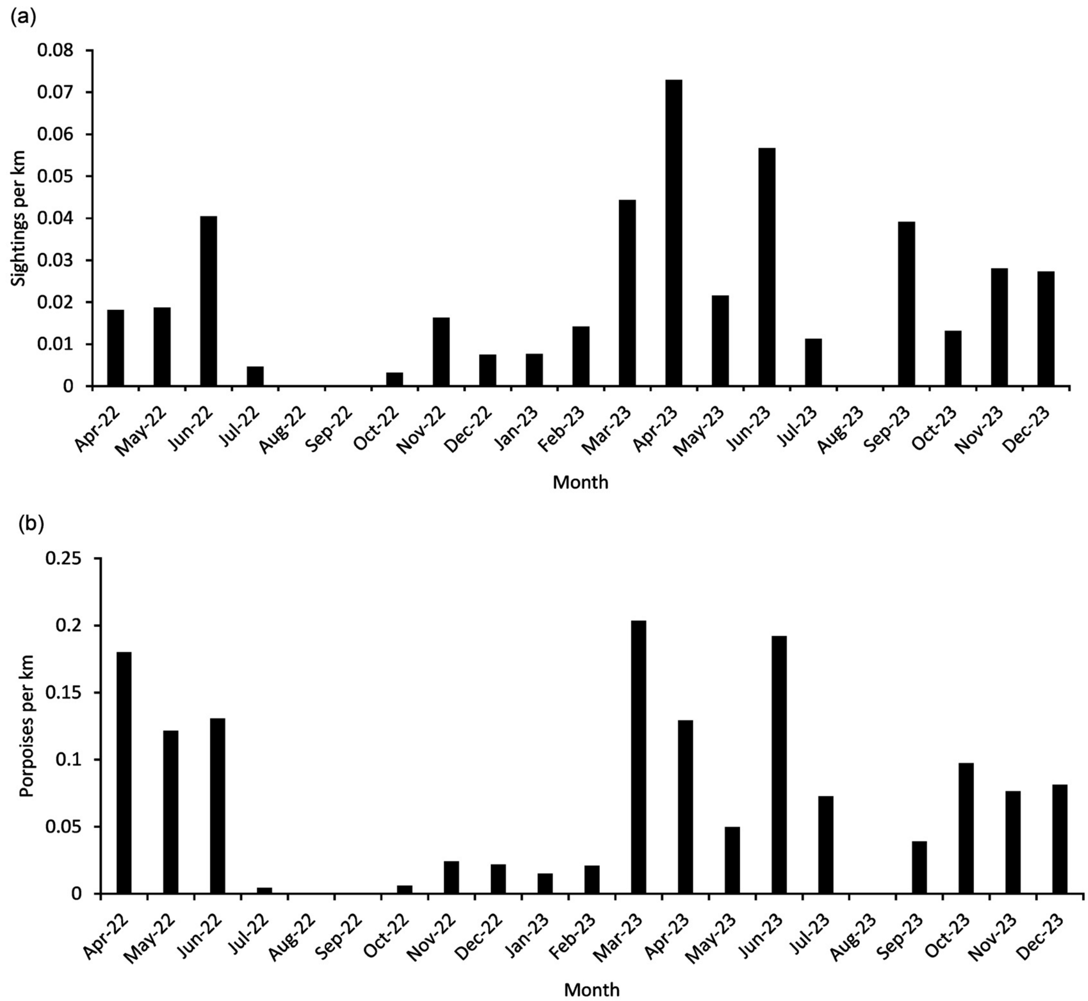

Figure 2. Monthly occurrence patterns of the East Asian finless porpoise in northern Aki Nada of the Seto Inland Sea, Japan. (A) sighting rates (sightings per km); (B) individual density (number of porpoises per km). No surveys were conducted in August 2023.

km) per day was 3.6 ± 1.1 (n = 52). The porpoise density did not significantly differ among oceanographic seasons (One-way ANOVA, F (3, 49) = 2.73, $p > 0.05$; Table 1), suggesting finless porpoises occupy most of northern Aki Nada throughout the year.

Sightings were spread throughout most of the survey area (Figs. 1B, 2), except for Zones I and VI, where we had no sightings. Sightings were most frequent north of Nagashima IsIsland and Usujima Island (Zone II), north of Kami-Kamagarijima Island (Zone IV), between Oyokoshima Island, and the eastern coast of Osaki-Kamijima Island. (Zone VII), between the northeastern tip of Osaki-Kamijima Island. and Oshibajima Island (Zone III), and the areas west and south of Abashima Island. (Zone IX). There was no significant difference in the area use among all survey zones across all oceanographic seasons (Kruskal-Wallis test, df = 3, $H = 2.73$, $p = 0.4$) (Fig. 3). Likewise,

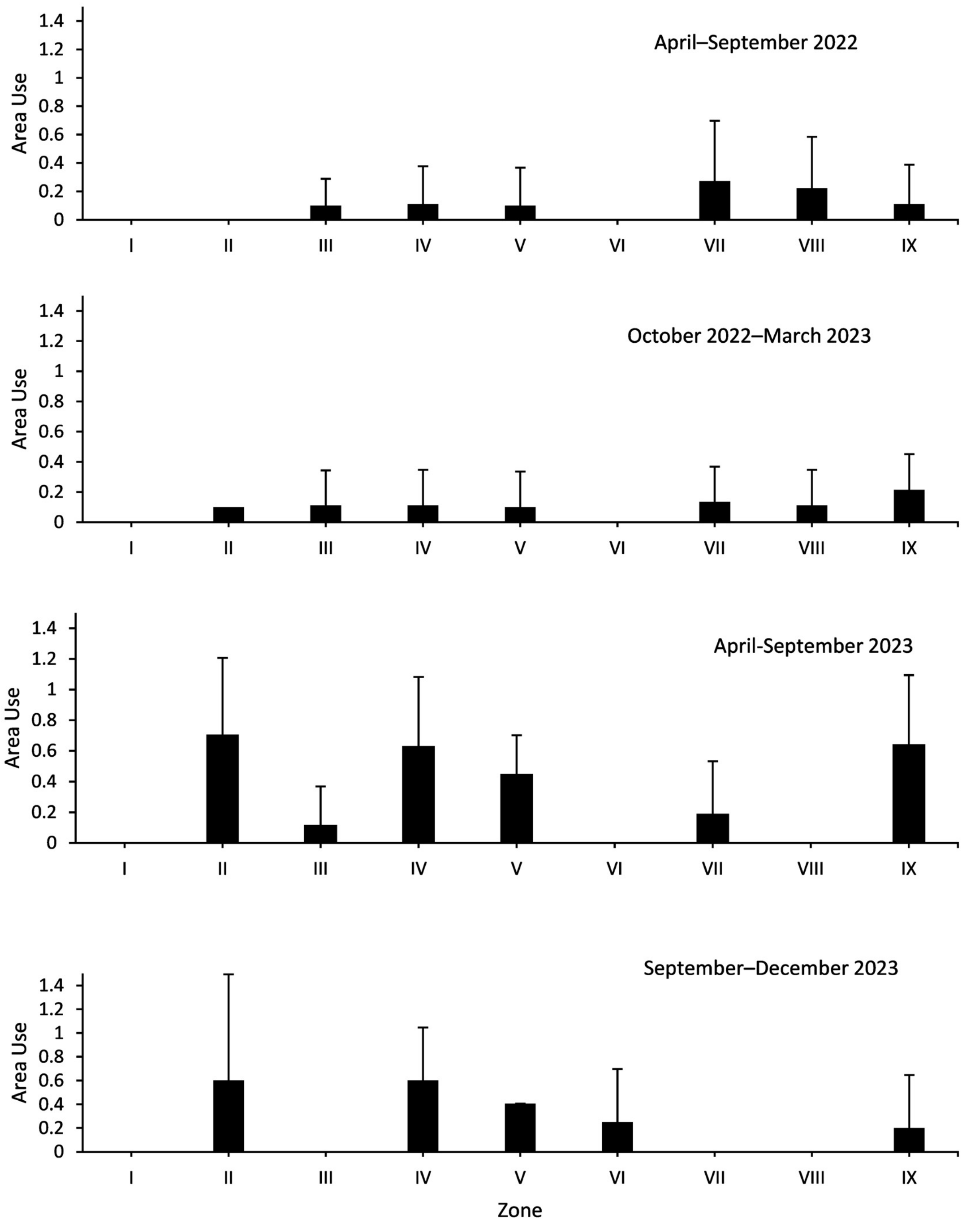

Figure 3. Area use indices for the East Asian finless porpoise distributed across survey zones in northern Aki Nada throughout four survey seasons.

calves were present in almost all the areas where we had sightings, except west of Akashi of Osaki-Kamijima Island. (Zone V) (Fig. 4). There was no significant difference in the calves encountered in all the zones across all oceanographic seasons (One-way ANOVA, $F(3,35) = 0.54$, $p = 0.7$).

Sightings of finless porpoises occurred in depths ranging from 5.5–83.3 m (44.39 ± 18.89 m, n = 52), and distances from shore ranging from 169.20–2,314.05 m (1,019.18 ± 505.49 m, n = 52) (Fig. S2). The GAM analysis resulted in identifying the model with substrate, depth, distance from shore, and sea surface temperature as factors having significant influences on porpoise presence and absence (Log-likelihood ratio test: $\chi^2 = 91.53$, df = 15.35, $p < 0.001$, Table S2A). On the other hand, location, substrate, depth, distance from shore, and surface temperature were identified as factors having significant influences on estimated group size (Log-likelihood test:

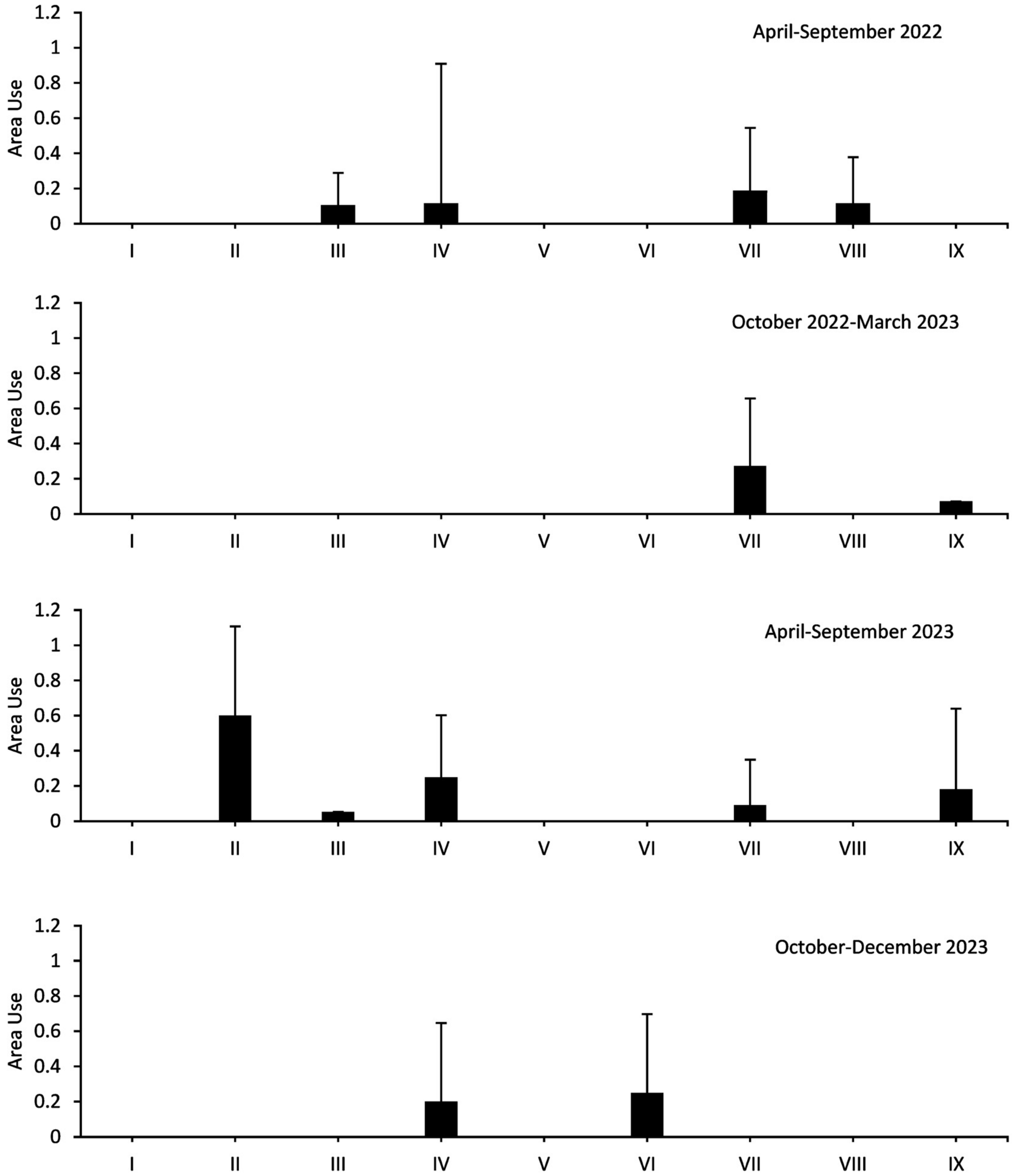

Figure 4. Area use indices of calves of East Asian finless porpoises distributed across survey zones in northern Aki Nada throughout four survey seasons.

χ^2 = 64.21, df = 19.95, p < 0.001, Table S2B). For calves, GAM analysis identified location, substrate, depth, and distance from shore as influential factors on their presence (Log-likelihood test: χ^2 = 80.64, df = 21.69, p < 0.001, Table S3A), while the number of calves was significantly influenced by location, substrate, depth and distance from shore only (Log-likelihood test: χ^2 = 45.81, df = 11.79, p < 0.001, Table S3B).

Group size and composition

Of the 52 sightings we encountered, this was composed of approximately 170 subgroups, with an average of 2.8 ± 2.5 porpoises for each subgroup (max. 21 individuals, n = 170). Each sighting comprised an average of 2.4 ± 4.7 subgroups (n = 170, Tables 2, S4).

The majority of subgroups were composed of pairs (37.06 %, n = 63), followed by singletons (25.9%, n = 44), trios (20.6%, n = 35), and then groups composed of more than three individuals (16.5%, n = 28/170) (Fig. 5). There was no significant difference in the subgroup sizes across seasons (One-way ANOVA, F (3, 170) = 0.55, p = 0.7; Table 2).

Table 2

Group and subgroup compositions of the East Asian finless porpoise in northern Aki Nada of the western Seto Inland Sea, Japan across survey seasons.

	Group size (No. of inds.)	No. of subgroups per sighting	Subgroup size (No. of inds.)	Calves per subgroup (No. of inds.)
April–September 2022	5.7 ± 4.3 (9)	1.7 ± 0.9 (9)	3.4 ± 3.2 (15)	1.1 ± 0.4 (15)
October 2022–March 2023	2.7 ± 1.9 (10)	1.3 ± 1.0 (10)	2.5 ± 1.6 (16)	1.0 ± 0.0 (16)
April–September 2023	3.6 ± 4.1 (22)	2.1 ± 1.6 (22)	2.8 ± 2.7 (114)	1.0 ± 0.0 (114)
October–December 2023	5.4 ± 4.0 (9)	4.1 ± 8.7 (9)	2.3 ± 1.4 (26)	1.0 ± 0.0 (26)
Mean	4.3 ± 4.2 (12.5)	2.4 ± 4.7 (12.5)	2.8 ± 2.5 (171)	1.0 ± 0.2 (171)

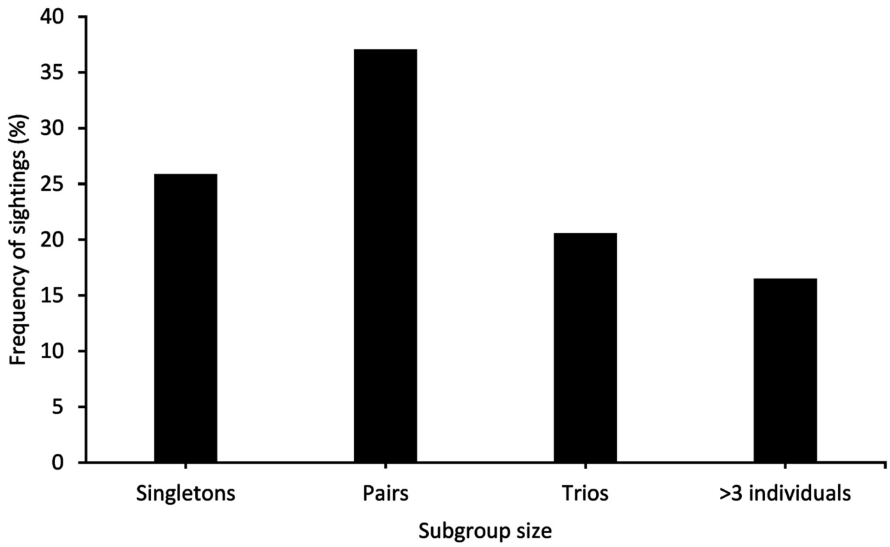

Figure 5. Subgroup composition of the East Asian finless porpoise in northern Aki Nada of the Seto Inland Sea, Japan (n = 52 sightings).

The maximum group size of 21 finless porpoises was observed on 19 September 2023 (Fig. 6), between Nagashima Island, Usujima Island, and Akitsu (Zone II; Figs. 1, 3). During that encounter, we recorded approximately 34 subgroups with group sizes ranging from 1 to 15 individuals during each surfacing event (Table S4). However, subgroup composition appeared fluid, and it was very likely that some individuals mixed with other subgroups, but we could not confirm this without individual identification. The supergroup was mostly composed of adults, but we were able to record at least three mother-calf pairs separate from the supergroup. We also detected schools of clupeids when we encountered these large groups in the same area. We did not observe fish-chasing behavior at the surface, but socio-sexual behaviours, including copulatory attempts, were observed.

Aside from the months with no sightings (August and September 2022; no survey was done in August 2023), mother-calf pairs were seen from April to July and November 2022, February to July, September and November 2023 (Fig. 7). Mother-calf pairs were highest during April 2023, followed by November 2022, then March 2023 (Fig. 7). We found no significant difference in the number of calves observed per km across oceanographic seasons (One-way ANOVA, $F(3, 49) = 2.15$, $p = 0.1$; Table 2).

Calves were present in 30% (n = 51/170) of the subgroups we observed. Of all subgroups with mother-calf pairs, 21.57% (n = 11/51) of these were followed by at least one other adult, often a male attempting to mate (Fig. 8). Such mating groups were observed in May 2022, March to June 2023, and September 2023.

DISCUSSION

Distribution pattern

East Asian finless porpoises were detected in northern Aki Nada throughout our 2022–2023 study period. Although employing different survey methods, our results agree with those of Kasuya and Kureha (1979),

Figure 6. A superpod of East Asian finless porpoises composed of approx. 12 individuals, taken on 19 September 2023 at Zone II.

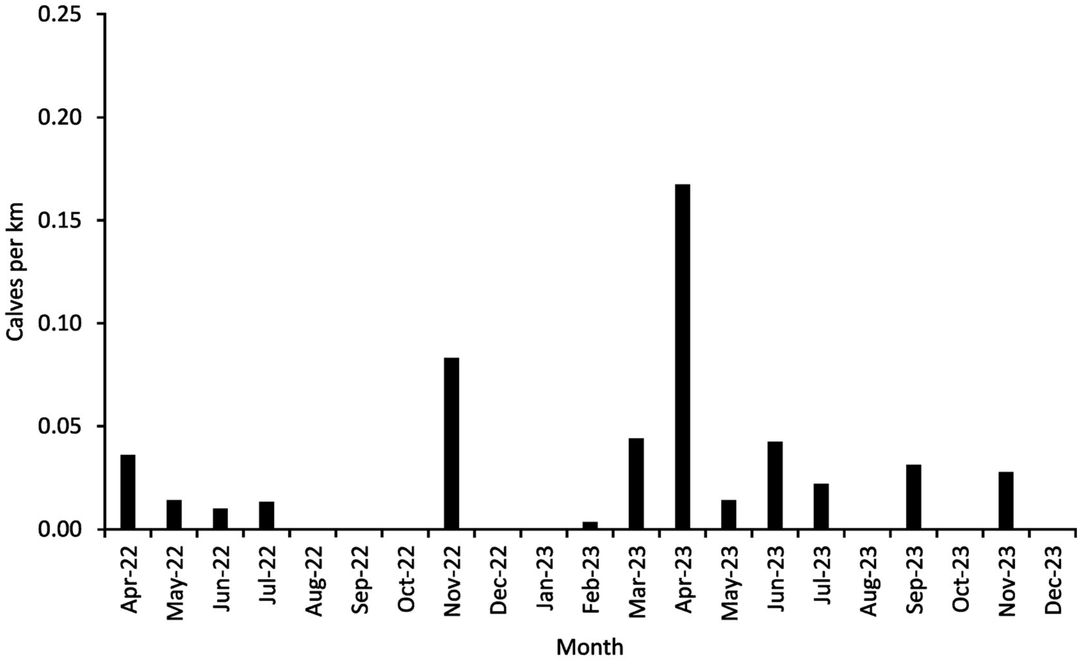

Figure 7. Monthly occurrence patterns of calves of the East Asian finless porpoise in northern Aki Nada of the Seto Inland Sea. Mean values of the number of calves per km are shown.

indicating that the northern Aki Nada area remains a viable habitat for the finless porpoise. Their current presence here is a positive development compared with the studies by Kasuya *et al*. (2002) and Shirakihara *et al*. (2007), both of which reported the porpoises' disappearance in Aki Nada during boat and aerial surveys conducted in 2000. The apparent disappearance noted in these previous studies was speculated to result from the porpoises' temporary migration out of northern Aki Nada due to either environmental deterioration, a shift in prey dynamics, or a combination of these and other factors (Shirakihara *et al*., 2007). Limitations in survey methodology for detecting such elusive animals may also have contributed to the difference in sighting rates, but this does not explain why finless porpoises were detected in other areas outside of Aki Nada during both their surveys.

Figure 8. A male (left) East Asian finless porpoise attempting to mate with a female (right), with a calf (centre). Recorded on 24 May 2022 at Zone IV.

Likewise, resightings of finless porpoises in northern Aki Nada follow a similar trend in the eastern side of the Seto Inland Sea, particularly in northern Harima Nada (Kondo, 2015). During ferry boat surveys conducted from 2010 to 2012, Kondo (2015) reported even higher encounter rates than the original surveys of Kasuya and Kureha (1979) and its succeeding surveys in 1999 and 2000, particularly in areas between Himeji and Sodoshima Island (Kasuya *et al*., 2002; Kondo, 2015), hinting at a possible population recovery in these areas.

The temporal and spatial distribution of finless porpoises across the study site was strongly influenced by several factors, including substrate, depth, distance from shore, and sea surface temperature (Table S2). These factors likely dictate the distribution of their prey, thus also directly influencing their habitat preferences (Karczmarski *et al*., 2000; Lechwar *et al*., 2023; Todd & Williamson, 2022). The substrate in northern Aki Nada was predominantly composed of a mixture of sand, mud, and shellfish beds, which is typical of finless porpoise habitats in other parts of Japan (Kasuya, 2017). Although our drones seldom observed surface foraging in these areas, long synchronous dives may indicate foraging on the bottom or within the water column. Stomach analyses of stranded porpoises from different parts of Japan and China have shown a diet that includes prey associated with sandy and muddy habitats, such as cephalopods, crustaceans, and burrowing, demersal, and epipelagic fishes (Barros *et al*., 2002, Shirakihara *et al*., 2008). Suitable conditions for a foraging site may be related to the stable occurrence of the finless porpoise in northern Aki Nada.

Our high sighting rates of finless porpoises from spring to summer (Fig. 2) are somewhat similar to those reported by Kasuya and Kureha (1979), whose sightings in the nearshore stratum (0.0–1.609 km from the coast) peaked from March to June. On the eastern side of the Seto Inland Sea, finless porpoise sightings also had the highest numbers between March and June (Kondo, 2015). We had no sightings from August until September 2022 (Fig. 2), which somewhat agreed with the observations of Kasuya and Kureha (1979), who reported their lowest densities between May and September, and Kondo (2015), whose sightings of finless porpoises in northern Harima Nada dropped during September of 2010 and 2011, but gradually increased from October onwards. One of the finless porpoises' preferred prey, the Japanese sand lance (*Ammodyes japonicus*; Ammodytidae), spawns in winter and starts estivation by burrowing in the sand when water temperatures reach 17–20°C (around June to July in the Seto Inland Sea, see Fig.S1A) (Endo *et al*., 2019), which could prompt finless porpoises to seek other kinds of prey (Kasuya & Kureha, 1979; Lu *et al*., 2016; Tomiyama & Yanagibashi, 2004). It has been suggested that finless porpoises may temporarily leave northern Aki Nada or move to deeper offshore areas because they prefer lower water temperatures (Kasuya, 2017). Similarly, the change in the sighting pattern of the finless porpoise, peaking in April before declining towards August (Fig. 2), is also comparable with the observations of

Shirakihara *et al*. (1994) during ferryboat surveys inside Ariake Sound and the adjacent Tachibana Bay in Nagasaki, Japan, and Kondo (2015) during ferry boat surveys in northern Harima Nada. Seasonal movement of the porpoises between the Ariake Sound and Tachibana Bay was suggested when sightings at the mouth of Ariake Sound and Tachibana Bay increased while sightings inside the sound decreased during the summer.

Interestingly, our sightings of finless porpoises remained high even towards the end of summer 2023, with a maximum of 21 individuals in one subgroup during September (Fig. 6). Similarly large groups of finless porpoises, comprising over 100 individuals, were reported chasing schools of small fishes, including Japanese anchovy (*Engraulis japonicus*; Engraulidae), Japanese shad (*Sardinella zunasi*; Dorosomatidae) and the dotted gizzard shad (*Konosirus punctuates*; Clupeidae) during the warm season in waters adjacent to the study site, particularly in June 2012 in southern Hiroshima Bay and off the coast of Hikari City, Suo Nada, in the western side of the Seto Inland Sea (Chugoku Shimbun, 2012). Because of these observations, it is possible that our low sighting rates during the summer of 2022 were due to finless porpoises aggregating to form larger and more concentrated subgroups to follow more mobile, schooling fish, possibly beyond northern Aki Nada. Their movement patterns in the wider area of the Seto Inland Sea during the summer await further investigation.

The majority (60%) of our sightings of finless porpoises occurred within 1 km from shore, while only 8% were in areas more than 2 km from shore (Fig. S2). The depth and distance patterns in our sightings align with those observed by Kasuya and Kureha (1979), indicating that finless porpoises are more likely to be concentrated in nearshore and shallow areas. Similarly, 70% of our sightings occurred in water depths 50 m and below (Fig. S2), consistent with the sighting distribution of other subpopulations in Japan (Amano *et al*., 2003, Kasuya & Kureha, 1979; Shirakihara *et al*., 2007; Shirakihara & Shirakihara, 2013; Kondo, 2015). Li *et al*. (2023) also found a distribution concentrated in waters less than 15 km from shore for finless porpoises surveyed in the Shandong Peninsula of the Yellow Sea in China. Similarly, higher sighting rates for finless porpoises were found in inshore waters than offshore waters (categorised by longitude from the mainland) on the west coast of Korea (Park *et al*., 2007, Park *et al*., 2015). In northern Aki Nada, this distribution may also be attributed to the narrow distances between islands, which are so close to each other that few areas are open and wide enough to qualify as 'offshore', and the average depth of northern Aki Nada is only around 39.9 m (International EMECS Centre, 2008). Such preferred habitats provide safer refuge from large predators, such as sharks (Okamura *et al*., 2024), and gentler environmental conditions compared with the open sea, especially when rearing calves. Furthermore, the prey preferences of finless porpoises, as previously mentioned, are associated with nearshore and shallow habitats, which may also affect their habitat distribution.

Group size and composition

The average subgroup size reported here (2.75 individuals) is somewhat larger than that observed by Shirakihara *et al.* (2007), who reported an average group size of 1.56 individuals during aerial surveys, and Kasuya and Kureha (1979) who reported 2.01 and 1.60 individuals during ferryboat surveys from March to September and October to February, respectively, in the Seto Inland Sea. Our oceanographic seasonal average values (range = 2.3–3.4 individuals, Table 2) are still higher than Kasuya and Kureha (1979). They are also higher than most group size estimates in other subpopulations throughout Japan, which used aerial and boat surveys, and range between 1.61 in Ise and Mikawa Bays (Miyashita *et al*., 2003) and 1.81 in Chiba-Sendai Bay (Amano *et al*., 2003). Likewise, group sizes in the Shandong Peninsula, China, averaged 1.74 individuals (CV = 3.69 at 95% CI), while inshore and offshore group sizes from the west coast of Korea were reported at 2.16 (CV = 0.16) and 1.24 (CV = 0.07) individuals, respectively (Park *et al*., 2015; Li *et al*., 2023). These comparisons suggest that Aki Nada may be crucial in the social interactions of finless porpoises, and the complexity of social structures among different populations remains to be investigated. In Misami West Port in Ariake Sound, Morimura and Mori (2019) were able to report an average group size of 6.7 ± 1.2 individuals (although they described it as an 'aggregation' rather than a group) with the use of a drone, which suggests drones may provide a better perspective than boat and aircraft surveys when examining group sizes or that porpoises tended to aggregate in more coastal areas.

The maximum group size of 21 individual finless porpoises reported here (Fig. 6) is among the higher maximum group sizes reported in other populations in Japan. Higher group sizes reported include 117 and 82 individuals reported by Yoshida *et al.* (1997) during an aerial survey in February in Tachibana Bay, and a group of more than

50 individuals in Ariake Sound as reported by Morimura *et al.* (2023), where they discuss the possibility that it was an aggregation of smaller subgroups. An aggregation of around 100 porpoises was also documented from a helicopter by a photographer from Chugoku Shimbun (2012) in Hiroshima Bay. Since encountering groups as big as the 19 September 2023 supergroup (Fig. 6) was rare in our study, it is possible that such encounters were either feeding or social aggregations, but not necessarily stable social groups. Nonetheless, these observations support the hypothesis that finless porpoise sociality may be more complex than previously predicted (Sakai *et al*., 2011; Fox *et al*., 2017; Terada *et al*., 2022; Morimura *et al*., 2023; Terada *et al*., 2024). More research may be needed to explore this.

Kasuya and Kureha (1979) reported observing mother and calf pairs usually accompanied by at least one or two adults, often males attempting to mate (Fig. 8). In northern Aki Nada, such mating groups were also observed from March to September, suggesting that finless porpoise breeding occurs from spring to late summer. Observations of calves were highest in April 2023, and since finless porpoises are predicted to have a gestation period of 11–12 months, parturition is expected to almost coincide with the mating season (Kasuya & Kureha, 1979). Most mother-calf pairs were particularly associated with the islands of Nagashima, Usujima, Abashima and Oyakoshima (Fig 4). The presence of mother-calf pairs and nursing groups in this area suggests that northern Aki Nada is an important breeding, calving, and nursing area for finless porpoises.

Conservation implications

Our results show that northern Aki Nada appears to be an important habitat for finless porpoise survival and social life in the Seto Inland Sea. Abashima Island was historically important to finless porpoise conservation, designated as a National Monument in the 1930s due to their high density here, and because local fishers used the presence of finless porpoises to indicate the presence of sea bream (Kasuya, 2017). It can also be noted that great efforts have been made since the 1970s to improve habitat quality through the Special Law for the Conservation of the Environment of the Seto Inland Sea and the banning of sea-sand dredging in the Seto Inland Sea in 2006 (International EMECS Centre, 2008; Nishijima, 2018). These factors make the Seto Inland Sea, particularly the Aki Nada Region, an ideal candidate to become one of Japan's Important Marine Mammal Areas (IMMA) (Notarbartolo di Sciara *et al*., 2016; Tetley *et al*., 2022).

Recent surveys of the Yangtze finless porpoise (*Neophocaena asiaorientalis orientalis*) show that populations have stabilised in Poyang Lake and slightly increased in Dongting Lake in China (Huang *et al*., 2020). However, there are still concerns that bridge constructions have affected their current habitat use and movement between lakes and the adjoining Yangtze River (Huang *et al*., 2020). Finless porpoises in the Seto Inland Sea may have also been affected by similar circumstances in the past (Shirakihara *et al*., 2007), but recent resightings in areas where they were reported to have disappeared, including in northern Aki Nada and northern Harima Nada (Kondo, 2015), may be a good indicator of the species' resilience. Further investigation of finless porpoises' movement patterns and occurrence in adjacent habitats is recommended, particularly Hiroshima Bay, southern Aki Nada, and Iyo Nada. Continuous monitoring of the finless porpoise in northern Aki Nada, including tracking strandings along the coasts and employing other means to detect finless porpoises (e.g., citizen science, acoustic monitoring, environmental DNA), will be crucial to develop and prioritise conservation measures for this endangered species.

AUTHOR CONTRIBUTIONS

M. de la Paz, H. Sato, T. Oyama and Y. Sakai participated in the conceptualisation of this research, while M. de la Paz, H. Sato, T. Oyama, A. Macario, S. Iwasaki and Y. Sakai contributed to the fieldwork and data collection. M. de la Paz, H. Sato, T. Oyama, A. Macario and Y. Sakai contributed to the data analysis and writing of the manuscript.

ETHICAL STATEMENT

All procedures performed in this study followed the Guidelines for the Proper Conduct of Animal Experiments and related activities laid down by the Hiroshima University Animal Research Committee (no. 004A200821, certified on 21 August 2020, and 100A230808, certified on 8 August 2023), the Guidelines for the Treatment of

Animals in Behavioural Research and Teaching by the Association for the Study of Animal Behaviour and the Guidelines for Ethological Studies by the Japan Ethological Society.

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Supplementary Material

(a)

(b)

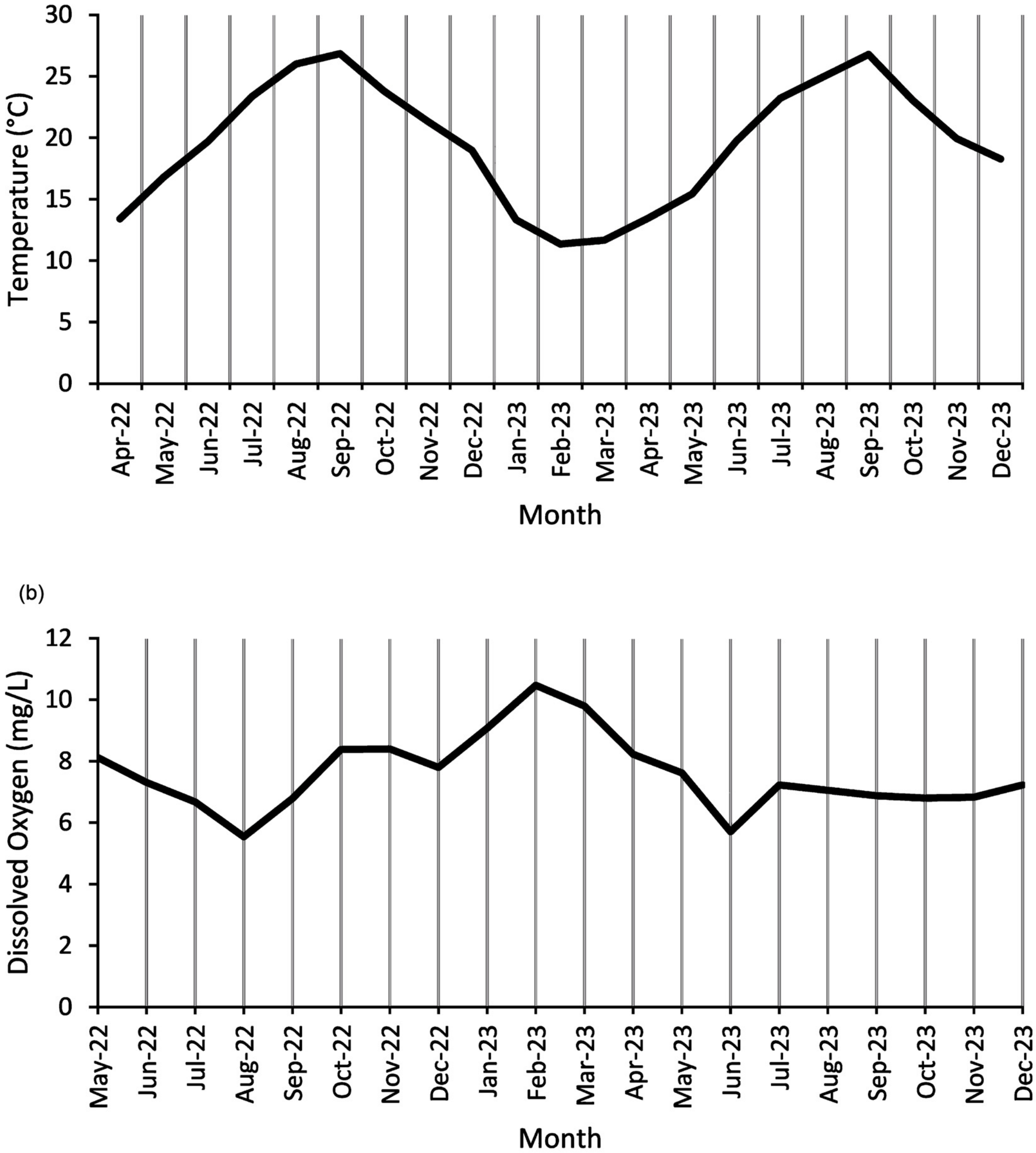

Figure S1. Monthly environmental parameters: (A) temperature and (B) dissolved oxygen in the northern Aki Nada from April 2022 to November 2023.

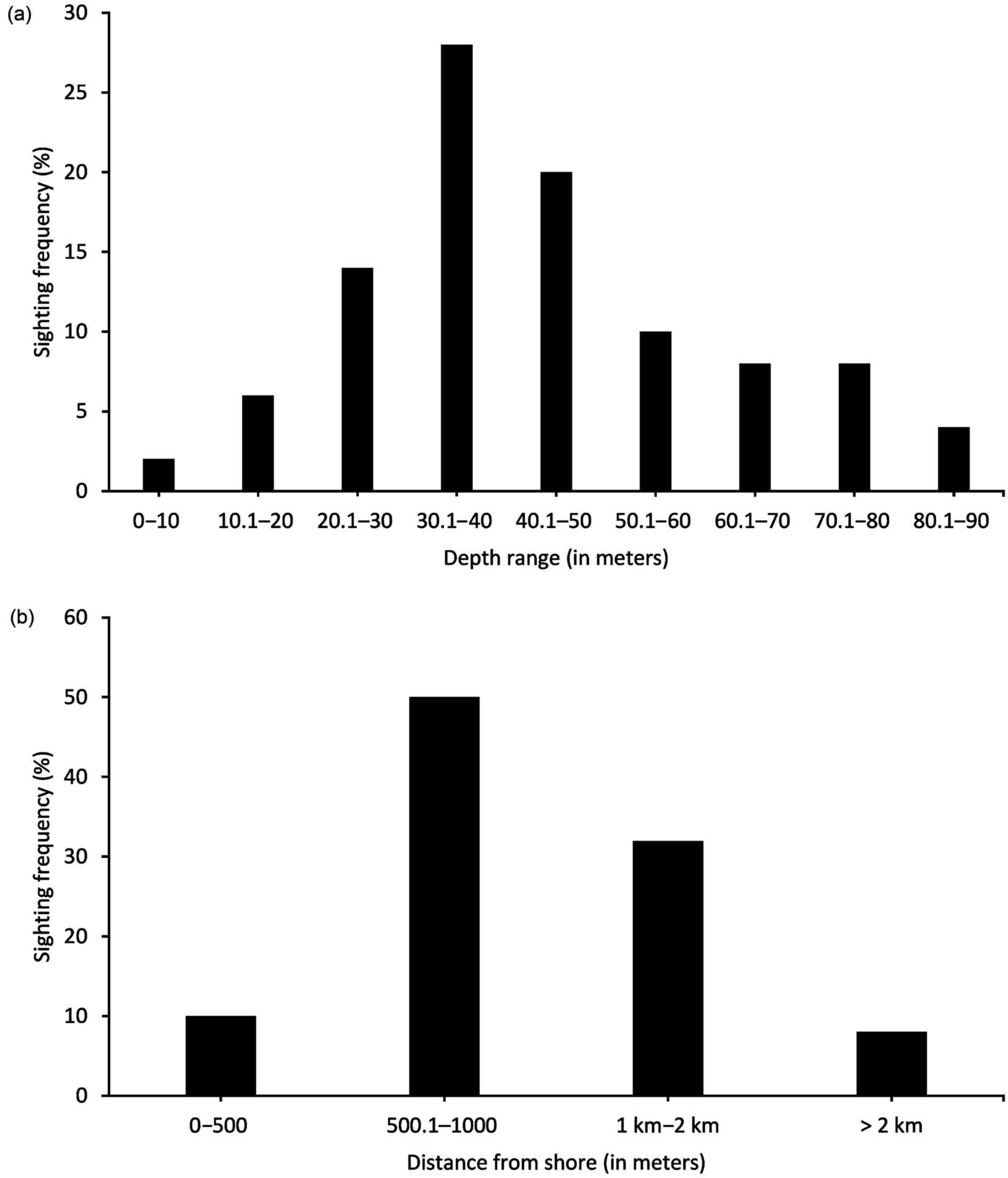

Figure S2. Distribution of sightings of the East Asian finless porpoise in northern Aki Nada of the Seto Inland Sea, Japan in relation to (A) depth range and (B) distance from shore.

Table S1

Average survey efforts of boat census surveys for the East Asian finless porpoise in northern Aki Nada of the western Seto Inland Sea, Japan, in terms of hours spent and distance covered for every oceanographic season.

	Survey effort (hours)	Distance covered (km)
April–September 2022	4.5 ± 1.1 (14)	66.7 ± 14.4 (14)
October 2022–March 2023	4.6 ± 1.8 (18)	50.9 ± 20.8 (18)
April–September 2023	3.9 ± 1.2 (15)	53.5 ± 16.9 (15)
October–December 2023	4.7 ± 0.4 (5)	71.3 ± 5.0 (5)

Mean ± SD values are shown with *n* inside parentheses

Table S2A

Generalised additive model output showing relationship between the East Asian finless porpoise's (a) presence/absence and (b) estimated group size with explanatory variables. Bold values indicate significance at $p < 0.05$.

Parametric coefficients	Estimate	Standard Error	Z value	p-value
Intercept	0.81	1.12	0.73	0.47
Substrate	–0.59	0.19	–3.11	**0.0019**
Approximate significance of smooth terms	Effective degrees of freedom	Reference degrees of freedom	Chi-square	p-value
Depth	2.11	2.69	9.9	**0.015**
Distance from shore	7.84	8.05	25.86	**0.0024**
Sea surface temperature	2.93	3.63	10.27	**0.036**
Salinity	1	1	1.78	0.18

R-sq.(adj) = 0.418; Deviance explained = 38.4%; UBRE = 0.4042; Scale est. = 1; n = 296

Table S2B

Generalised additive model output showing relationship between the East Asian finless porpoise's (a) presence/absence and (b) estimated group size with explanatory variables. Bold values indicate significance at $p < 0.05$.

Parametric coefficients	Estimate	Standard Error	Z value	p-value
Intercept	1.51	0.95	1.60	0.11
Location	–0.19	0.10	–1.96	**0.05**
Substrate	–0.44	0.16	–2.75	**0.006**
Approximate significance of smooth terms	Effective degrees of freedom	Reference degrees of freedom	Chi-square	p-value
Depth	2.92	3.64	16.39	**0.0021**
Distance from shore	5.46	6.43	22.36	**0.0016**
Sea surface temperature	3.94	4.85	21.52	**0.00069**
Salinity	1	1	0.49	0.48

R-sq.(adj) = 0.0518; Deviance explained = 48.5%; -REML = 218.97; Scale est. = 1; n = 296

Table S3A

Generalised additive model output showing relationship between the East Asian finless porpoise calves' (a) presence/absence and (b) number of calves with explanatory variables. Bold values indicate significance at $p < 0.05$.

Parametric coefficients	Estimate	Standard Error	Z value	p-value
Intercept	1.51	0.945	1.60	0.11
Location	–0.19	0.095	–1.96	**0.05**
Substrate	–0.44	0.161	–2.75	**0.006**
Approximate significance of smooth terms	Effective degrees of freedom	Reference degrees of freedom	Chi-square	p-value
Depth	2.92	3.642	16.387	**0.0021**
Distance from shore	5.46	6.434	22.362	**0.0016**
Sea surface temperature	3.94	4.846	21.522	**0.00069**
Salinity	1	1	0.491	0.48

R-sq.(adj) = 0.0518; Deviance explained =48.5%; -REML = 218.97; Scale est. = 1; n = 296

Table S3B

Generalised additive model output showing relationship between the East Asian finless porpoise calves' (a) presence/absence and (b) number of calves with explanatory variables. Bold values indicate significance at $p < 0.05$.

Parametric coefficients	Estimate	Standard Error	Z value	p-value
Intercept	0.46	0.79	0.58	0.56
Location	–0.23	0.08	–2.87	**0.0042**
Substrate	–0.45	0.13	–3.39	**0.0007**
Approximate significance of smooth terms	Effective degrees of freedom	Reference degrees of freedom	Chi-square	p-value
Depth	3.31	4.12	14.66	**0.0053**
Distance from shore	3.55	4.37	14.47	**0.0082**
Sea surface temperature	1	1	1.60	0.21
Dissolved Oxygen	1.29	1.53	2.14	0.21
Salinity	1	1	0.29	0.59

R-sq.(adj) = 0.269; Deviance explained = 40.5%; -REML = 95.285; Scale est. = 1; n = 296

Table S4

Group size, subgroup size, and number of calves for finless porpoise groups encountered from April 2022 to December 2023 in northern Aki Nada, Seto Inland Sea, Japan.

Date	Subgroup No.	Group No.	Group size (100 m chain rule)	Subgroup size (10 m chain rule)	No. of calves
26-Apr-22	1	1	10	5	1
	2			5	1
10-May-22	3	2	14	14	2
24-May-22	4	3	6	1	
	5			2	1
	6			3	
31-May-22	7	4	3	3	
21-Jun-22	8	5	3	3	
	9	6	1	1	
	10	7	7	3	
	11			4	1
	12	8	1	1	
27-Jul-22	13	9	6	2	1
	14			2	1
	15			2	1
3-Oct-22	16	10	2	2	
25-Nov	17	11	1	1	
	18	12	2	2	1
9-Dec-22	19	13	3	3	
16-Jan-23	20	14	2	2	
6-Feb-23	21	15	1	1	
	22	16	1	1	
	23	17	4	4	1
6-Mar-23	24	18	4	2	1
	25			2	
13-Mar	26	19	17	3	
	27			1	1
	28			2	
	29			4	1
	30			7	1
3-Apr-23	31	20	5	3	
	32			2	1
	33	21	3	2	
	34			1	1
	35	22	2	2	1
19-Apr-23	36	23	2	2	
	37	24	1	1	
15-May-23	38	25	10	3	1
	39			2	1
	40			1	
	41			1	
	42			3	1
	43	26	3	1	
	44			2	1
8-Jun-23	45	27	1	1	
	46	28	3	1	
	47			2	1
	48	29	2	1	
	49			1	
	50	30	2	2	
12-Jun-23	51	31	2	2	
	52	32	26	2	
	53			3	
	54			2	
	55			2	
	56			3	
	57			2	
	58			1	
	59			2	
	60			1	

Date	Subgroup No.	Group No.	Group size (100 m chain rule)	Subgroup size (10 m chain rule)	No. of calves
	61			3	1
	62			1	
	63			3	
	64			1	
	65			2	
	66			3	
	67			3	
	68			2	
12-Jun-23	69			2	1
	70			2	
	71	33	33	2	
	72			4	
	73			2	1
	74			1	
	75			5	
	76			2	
	77			3	
	78			2	
	79			1	
	80			3	1
	81			1	
	82			3	
	83			2	
	84			1	
	85	34	27	3	1
21-Jun-23	86			1	
	87			3	1
	88			2	1
	89			2	1
	90			1	
	91			2	
	92	35	2	2	1
	93		1	1	
	94			2	1
25-Jul-23	95	36	6	3	1
	96			1	
	97			2	1
31-Jul-23	98	37	8	2	1
	99			3	
	100			1	
	101	38	4	2	1
	102			2	1
	103	39	3	3	
	104	40	4	2	
6-Sep-23	105			2	
	106			2	
	107			1	
	108	41	13	1	
	109			3	
	110			6	
	111			4	
	112			1	
	113	42	24	2	
	114			6	
	115			1	
	116			10	
19-Sep-23	117			10	
	118			2	
	119			5	
	120	43	132	7	
	121			2	
	122			1	
	123			1	

Date	Subgroup No.	Group No.	Group size (100 m chain rule)	Subgroup size (10 m chain rule)	No. of calves
	124			3	
	125			2	
	126			3	
	127			3	1
	128			4	
	129			2	
	130			2	
	131			2	
	132			1	
	133			1	
	134			15	
	135			3	
	136			8	
	137			5	
	138			3	
	139			5	1
	140			5	
	141			2	
	142			21	
	143			6	1
	144			8	
18-Oct-23	145	44	2	2	
	146	45	2	2	
	147	46	16	1	
	148			3	
	149			3	
	150			2	
	151			3	
	152			3	
	153			1	
14-Nov-23	154	47	1	1	
	155	48	30	3	
	156			1	1
	157			1	
	158			2	1
	159			2	1
	160			1	
	161			1	
	162			2	1
	163			2	
	164			7	1
	165			3	1
	166			5	2
	167	49	2	2	1
	168	50	2	2	1
6-Dec-23	169	51	4	4	
	170	52	2	2	
Average Range S.D.				2.8 1–21 2.5	1.0 1–2 0.2