Local extinction of an isolated dugong population near Okinawa Island, Japan

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Abstract

A small animal population becomes extinct owing to demographic and environmental stochasticity after declining below the minimum viable population (MVP). However, the actual process of extinction derived by stochastic factors after crossing MVP has not been recorded for long-lived marine mammals. Here, we reconstructed the extinction history of a small, isolated population of dugongs in Okinawa over 125 years. The initial population size of 300 in the 19th century declined to 50 in 1916 (because of overfishing), 20 in 1979, 10 in 1999, 3 after 2006, and finally extinct in 2019. After 1979, a decline in the natural growth rate for only 20 individuals led to extinction. Long-lived animals fall below the MVP; thus, active conservation measures should have been taken much sooner than when the actual extinction happened.

Introduction

Sustainability and extinction of a small animal population is determined by extrinsic (e.g., hunting and habitat loss) and intrinsic (e.g., stochastic reproduction and mortality) factors[1, 2]. In general, human-induced extrinsic factors first reduce the population size to a minimum viable population (MVP); then, demographic and environmental stochasticity leads to final extinction. Extinction probability is estimated by population viability analysis (PVA), and the MVP is generally estimated as approximately 50 (ref. [3]). However, the actual history of a population decrease to extinction with causal factors has not yet been recorded, particularly for long-lived marine mammals; such study requires a long observation period, although many of these species are at the edge of extinction. From this perspective, effective measures to avoid species extinction should be taken based on the practical number of MVP along with possible extinction drivers. In this study, we reconstruct the extinction history of a small, isolated population of dugongs in Okinawa for over 125 years.

The dugong (*Dugong dugon*) is a marine mammal inhabiting tropical seagrass meadows for feeding grounds. It is a flagship species for tropical marine ecosystems and is currently classified as 'vulnerable' on the IUCN Red List[4]. As the population has declined because of hunting, coastal development, and habitat destruction, effective conservation measures need to be addressed[5]. The average natural life span of dugongs is not known; the oldest specimen is suggested to be 73 years old, and only one-tenth of the population is 36 years old or more[6,7,8]. Dugongs mature at 9 to 10 years of age and give birth to calves with an interval of three to seven years. The population growth rate is suggested to be 5%, corresponding to the life history presented in this study.

The largest known population of dugongs is located in the coastal waters of northern Australia, comprising almost 70,000 individuals[8]. In southeast Asia, dugongs inhabit coastal waters near Indonesia, Malaysia, and Thailand, and a few hundreds to a thousand individuals live in each country (Fig. 1a). In the Philippines, dugong populations are fragmented and, in Taiwan, they have become locally extinct[9]. A small population of dugongs has been found in the coastal waters of Okinawa Island, part of the Ryukyu Islands of Japan—in the northern part of the dugong distribution in the western Pacific—since, at least,

the 17th century. From the 17th to 19th centuries, dugongs were hunted as a tax to the Ryukyu Dynasty in the Yaeyama Islands—the southernmost islands in the Ryukyus—in a period when hunting was sustainable and maintained the dugong population (Fig. 1b, c, d). However, after the Ryukyu Dynasty collapsed and was integrated into Japan in 1879, dugongs began to be harvested commercially.

Results

The harvest statistics from 1893 to 1916 showed that more than 300 dugongs were caught during this period near the Yaeyama, Miyako, and Okinawa Islands (Fig. 2d, Extended Data Fig. 1a, b)[10,11,12]. However, from 1911 onwards, the number of captures decreased, and the last reported individual captured was a calf near Okinawa in 1916, suggesting that hunting pressure resulted in a decrease in the population size. To reconstruct the decline of the dugong population in these islands, we applied a population dynamics model (see Methods). The minimum number of individuals in 1894 ranged from 318 to 364, which satisfies the population in 1917 > 50 (Extended Data Fig. 1a). If we assumed that the population in 1917 was > 20, the minimum number in 1894 ranged from 293 to 335, which would not be remarkably different from the scenario in which the initial number was > 50. If we assumed the initial number to be either than > 370 or < 290, then the population from 1894 to 1917 would show no significant reduction or would be near extinction, respectively. Therefore, we considered the initial population size in 1894 and 1917 to have been ca. 290−370 and 20−50, respectively (Fig. 2a).

No record of dugongs is available regarding 1917 to 1964; however, mortality was inferred to have increased because of the use of explosives (dynamite) to harvest fish and dugongs[12]. Such fishing continued after World War II, even though it was prohibited until 1972 (ref. [13]), when Okinawa Prefecture returned to Japan from US occupancy, and the dugong was designated as a natural monument of Japan. Since 1965, reports of hunting, bycatch, stranding, and dead bodies drifting ashore have been reported in local newspaper articles (Supplementary Table 1). Near Yaeyama and Miyako Islands, three dugongs were reported as hunted for commerce in 1965 and 1967, which reveals that dugong had been a fishery target at least by that time. In 1987, a dead specimen was found on Yaeyama shore, and no dugongs were observed on these islands—the Okinawa dugongs have been isolated (Fig. 2a).

From 1979 to 2004, 14 dugongs were found dead on Okinawa Island: seven were caught in gill or fixed nets (another four were released alive or bred in an aquarium), and seven dead bodies drifted ashore (Fig. 2e, Supplementary Table 1). Another dugong was found dead on shore at Kumamoto, 650 km north of Okinawa, from where it might have strayed[14]. Six dead individuals out of the 14 were calves 2 months to several years old. Interestingly, a pregnant female was caught in a fixed net in 1995, which shows that the Okinawa dugongs reproduced until 2002, given the existence of the calves. Bycatch continued until 1997, but no bycatch deaths have been reported since then.

The population size in 1979 was estimated using bycatch and stranding reports from 1979 to 2004, using a stochastic model (see Methods). At intrinsic rate of population increase (r) of 5%, 4%, 2%, 1%, and 0.1%, the number of dugongs in 1979 was estimated to be 12, 13, 18, 21, and 24 individuals, respectively

(Supplementary Table 2). With an r of ≥ 4%, the reported stranding mortality was unlikely to result in a significant decline in the population. However, if r ≤ 1%, the population was estimated to comprise approximately 20 individuals in 1979. This number is not the lowest limit of the population, but the median of the number in 1979, as the number in 2004 was 6.

Since 1997, aerial observations of the Okinawa dugongs have been intensively conducted, and 15 dugongs have been identified (Supplementary Data 1). In 1998, the most probable number of dugongs was 12. From 1999 to 2002, four dead bodies drifted ashore, and one dugong was caught dead in a gill net. Another four have not been observed since 2004 and 2006. Since 2007, only three individuals (hereafter referred as A, B, and C) have been identified, along the eastern and northwestern coasts (Fig. 3). Aerial surveys have covered dugong habitats all around Okinawa Island once a month from 2007 to 2009, and four times a year since 2009 (Extended Data Fig. 4). Whereas sea turtles have been found throughout the area, dugongs have been found only in specific waters, which supports the hypothesis that only three animals have been present since 2007 (Extended Data Fig. 5).

Dugong A was male and its observed tracks were restricted to 3 km offshore Kayo (Fig. 3b). Feeding trails had also been observed constantly in a seagrass meadow on a reef flat of Kayo. On the other hand, main habitat of dugongs B (female) and C (sex unknown) was identified in a bay between the main Okinawa Island and Kouri-jima Island (Fig. 3a). They were frequently observed swimming side by side suggesting dugong C was a calf of dugong B (Fig. 3). Dugong C sometimes migrated to the eastern side of Okinawa Island (in one case accompanied by dugong B), and was finally observed in June 2015. Dugong C might have migrated to a remote location, possibly to search for its own habitat or mate. Dugong A has not been observed since September 2018, and the feeding trails have not been observed since then. Dugong B was found dead as drifted ashore at Unten Port, on the south coast of Kouri-jima Island on 18 March 2019 (Extended Data Fig. 6). We are not certain that dugong A and C are dead. However, the three dugongs had been identified and observed since 2007, while none has been observed since 2018, suggesting the local Okinawa dugong population may have now become extinct at least from this area. Given that dugongs are able to make long-distance migrations (e.g., 560–1,000 km)[15,16], a more extensive search of a broader geographical area would be required to determine whether dugongs A and C (in particular the latter) still alive.

Discussion

The Okinawa dugong extinction is attributed to extrinsic factors such as hunting, bycatch, and habitat loss and to intrinsic factors such as demographic stochasticity. Overfishing was the first major driving force for the sharp decline of the Okinawa dugong from 300 individuals, during the early 20th century, to the estimated 20–50 individuals in the late 20th century. Dugong habitats have been lost because of coastal development, such as reclamation and port construction during this period. Moreover, the seagrass bed area decreased from 10,574 km^2 in 1979 to 10,554 km^2 in 1989 and 10,497 km^2 in 2012 accompanying with decrease in natural coastline (Fig. 2b, c and Extended Data Figs. 2, 3). The seagrass bed area in 1979 provided the lowest environmental carrying capacity for dugongs—10 to 20 at that time.

The reduced area in 2012 was still sufficient for the last three specimens in 2012. Therefore, we infer that the final extinction was caused by a reduction in the natural growth rate, which is assumed to be derived from genetic deterioration in the reduced population density.

We examined the impact of bycatch on the population decline between 1997 and 2019 using PVA (see Methods). The probability that $N_{1997} \leq 11$ depends on the population size in 1979, N_{1979}, when the harvest was banned. To obtain these probabilities acknowledging the scenarios under a combination of fecundity (s) and annual survival rate (f), we have: (s, f) = (0.97, 0.33), (0.95, 0.33), (0.97, 0.14), (0.923, 0.33), and (0.95, 0.17), with annual population growth rates (r) of 4.84%, 2.78%, 1.28%, 0.0%, and 0.21%, respectively. We conducted PVA using an individual-based model that describes the sex and age of each individual (Extended Data Fig. 7). Even if r was 2.8%, it is likely that the number of specimens had already decreased to < 17 in 1979. Unless it has been < 11 since 1979, the natural r during the 20th century would have been < 3%. Considering another scenario, even if the average natural r was 0% (unless it was negative), it is likely that the number of specimens had already decreased to < 25 since 1979.

As the number of dugongs declined from ca. 20 in 1979 to 12 in 1998, dugongs finally reduced to extinction in 2019. Thus, the critical MVP was assigned as 10–20 for the dugong population in this perspective. Although different in their life cycle parameters, a small subpopulation of Hawaiian monk seals experienced a decrease in the number of adults to 30 and then an increase to 100 within 10 years[17], which leads to a threshold MVP between 20 and 30. The Okinawa dugong had declined its population size to 20, and then intrinsic factor of reduced growth rate lead to extinction 40 years later.

Dugongs A and B must have been > 20 years old, because we identified them as adults in 2007. Given their long life cycle, the final extinction lags behind the MVP. As the population size crossed below the MVP, we should have taken conservation actions to increase the dugong population size in Okinawa, for example, by introducing dugongs from other populations or breeding them in captivity.

Methods

Population dynamics model. The following population dynamics model was applied to reconstruct the initial dugong population size in 1894 from fishery statistics between 1894 and 1914:

$$N_{t+1} = N_t (1 + r - r N_t / K) - C_t,$$

where r is the intrinsic rate of population increase, N_t is the population size in year t, K is the carrying capacity, and C_t is the number of individuals removed from the waters near the Ryukyu Islands in year t. The carrying capacity (K) in 1893 was sufficient to sustain the initial population of dugongs at that time (N_{1894}). The intrinsic rate of population increase (r) was given as 1%, 2%, 4%, or 5% within a range of natural one.

Stochastic model. We applied a stochastic model to estimate the number of individuals in 1979 from stranding and bycatch record with a binomial distribution because the number of reported deaths was

very small.

$$N_{t-1} = N_t - C_t \boxtimes \beta [N_t - C_t, r],$$

where C_t is the number of deaths in year t, $\beta [N_t - C_t, r]$ is a binomial number, and Prob $[\beta [N, r] = x] = {}_N C_x r^x$ $(1 - r)^{N-x}$. As it is a stochastic model, the number of individuals in 2004 varied among each run; the lower limit was N_{1979}, by which <50% of the runs reached $N_{2004} < 6$ individuals.

Population viability analysis. We conducted a population viability analysis (PVA) to evaluate the impact of bycatch on the population decline between 1997 and 2019 based on the stranding records. We denoted fecundity as f, the survival rate until 1 year old as s_0, the annual survival rate after 1 year old as s, the age at maturity as a_m, and the physiological longevity as A. We assumed that the fecundity f was 1/3 if at least one adult male existed in the population; the sex ratio at birth was 1:1 on average; the age at maturity a_m was 8 years of age[23], and the physiological longevity A was 73 years[6.] We ignored environmental stochasticity because no mass deaths caused by infectious diseases or changes in survival or mortality rates due to environmental fluctuations have not been recorded during this period. We also ignored density effects because the carrying capacity of the location was sufficiently greater than the initial population size, and our goal was to investigate the possibility of population recovery after a decrease in population using a population dynamics model and estimate the natural growth rate during this period. The detailed extinction risk depends on age structure.

According to the life history parameters, except the physiological longevity compiled by (ref. [23]), the annual survival probability of an a year-old individual is s for a = 1, 2, …, 72; for a = 0, and 0 for a = 73; the reproductive probability of an adult female >8 years old is $2f$. As the number of years for a population to become extinct or recover depends on age composition, age-specific survival, and reproductive rates, we obtain the population growth rate by the maximum eigenvalue of the following Leslie matrix, $\mathbf{L} = \{L_{ij}\}$ (i = 1,…20, j = 1,…,20) as:

$L_{i1} = s_0 f / 2$ for $i \geq a_m$, $L_{i+1,i} = s$ for i = 1,…, 72, and L_{ij} = 0 otherwise.

The population growth rate l was 2.3%, 0.3%, -0.4%, and -0.7% if (s, s_0) = (0.95, 0.8), (0.93, 0.8), (0.92, 0.8), and (0.95, 0.4), respectively.

We assumed that the sex of each individual in 1979 was randomly sampled by the 1:1 sex ratio, and its age was randomly sampled by the stable age structure that is given by the eigenvector of the Leslie matrix with the maximum eigenvalue. The probability that $N_{1997} \leq 11$ is >5% if $N_{1979} \leq 16$, $N_{1979} \leq 17$, and $N_{1979} \leq 23$, under the scenarios (s, f) = (0.95, 0.33), (0.97, 0.14), (0.95, 0.17), respectively. We assumed that the number of individuals at age 1 year in year $t + 1$, denoted by $N_{1,t+1}$, is determined by the binomial distribution:

$$\Pr[N_{1,t+1} = x] = \binom{N_f}{x} (s_0 f)^x [1 - (s_0 f)]^{N_f - x} \ ,$$

where N_f represents the number of adult females in year t. We assumed that no twins were born. We assumed that the probability that an individual with age x survived in the next year is s if x = 1 or s0 if x = 0. We also assumed that C_t individuals who died by bycatch were randomly chosen from any sex and age because the age of individuals caught by bycatch is rarely known. We do not know the sex of some individuals.

Data availability

All data in this study are included in this article and its supplementary data files.

Declarations

Acknowledgments

Author contributions

T.H. and N. A. conducted behavior analysis. H.Y. compiled and analyzed habitat data. H. M. conducted population analysis. H.K. organized and wrote the manuscript.

Competing interests

Authors declare that they have no competing interests.

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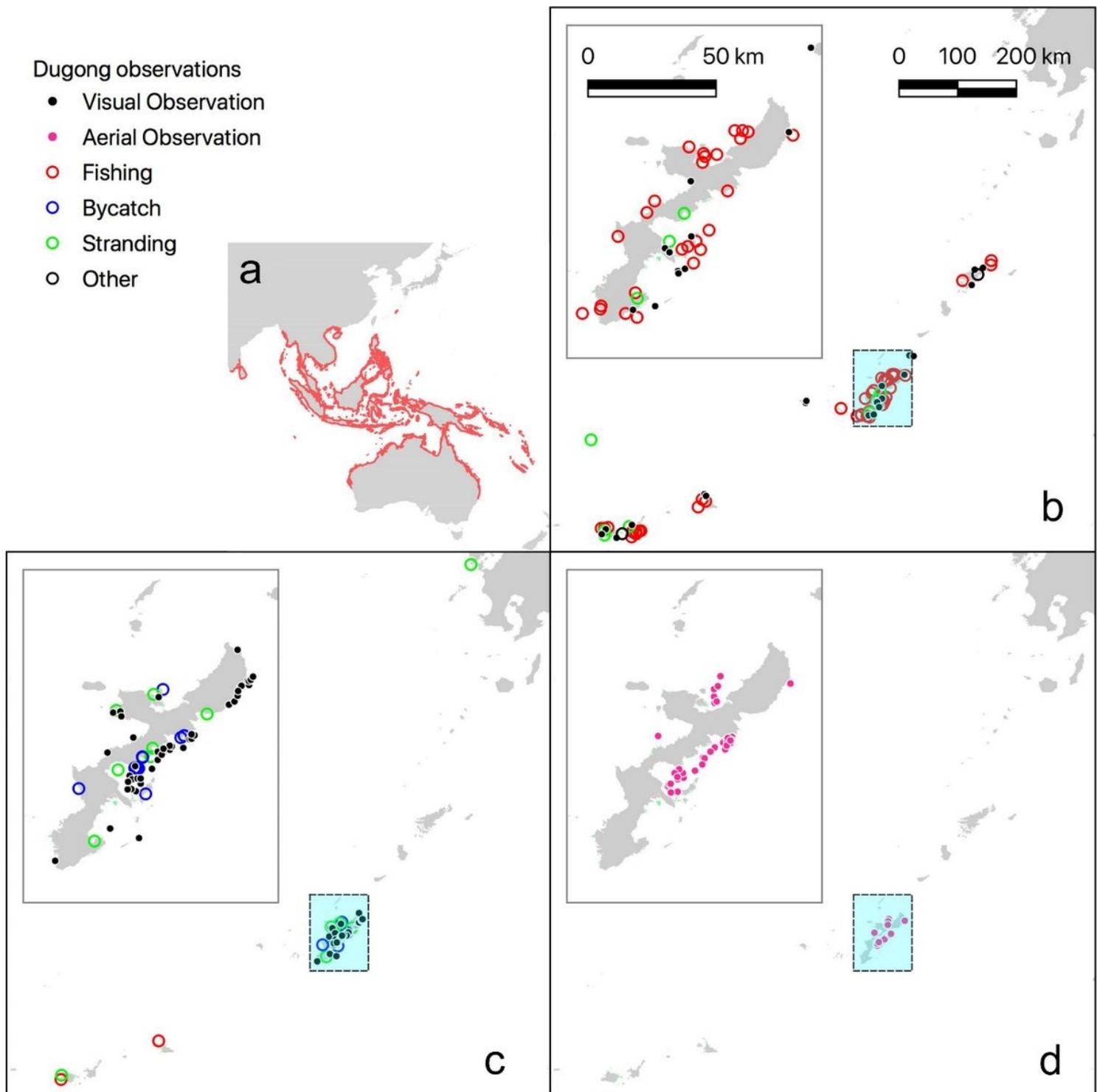
Figures

Figure 1

Observation and/or hunting records of dugongs. a, Distribution of dugongs in the southeast Asia and Australia. b, Historical dugong hunting and observation locations near the Ryukyu Islands before 1965. c, Visual observation and records of bycatch and stranding (dead body drifted ashore) since 1965. d, Aerial observation since 1997. The data from different observation are indicated by different-colored circles. The data were compiled from (refs. 10,18,19,20,21,22).
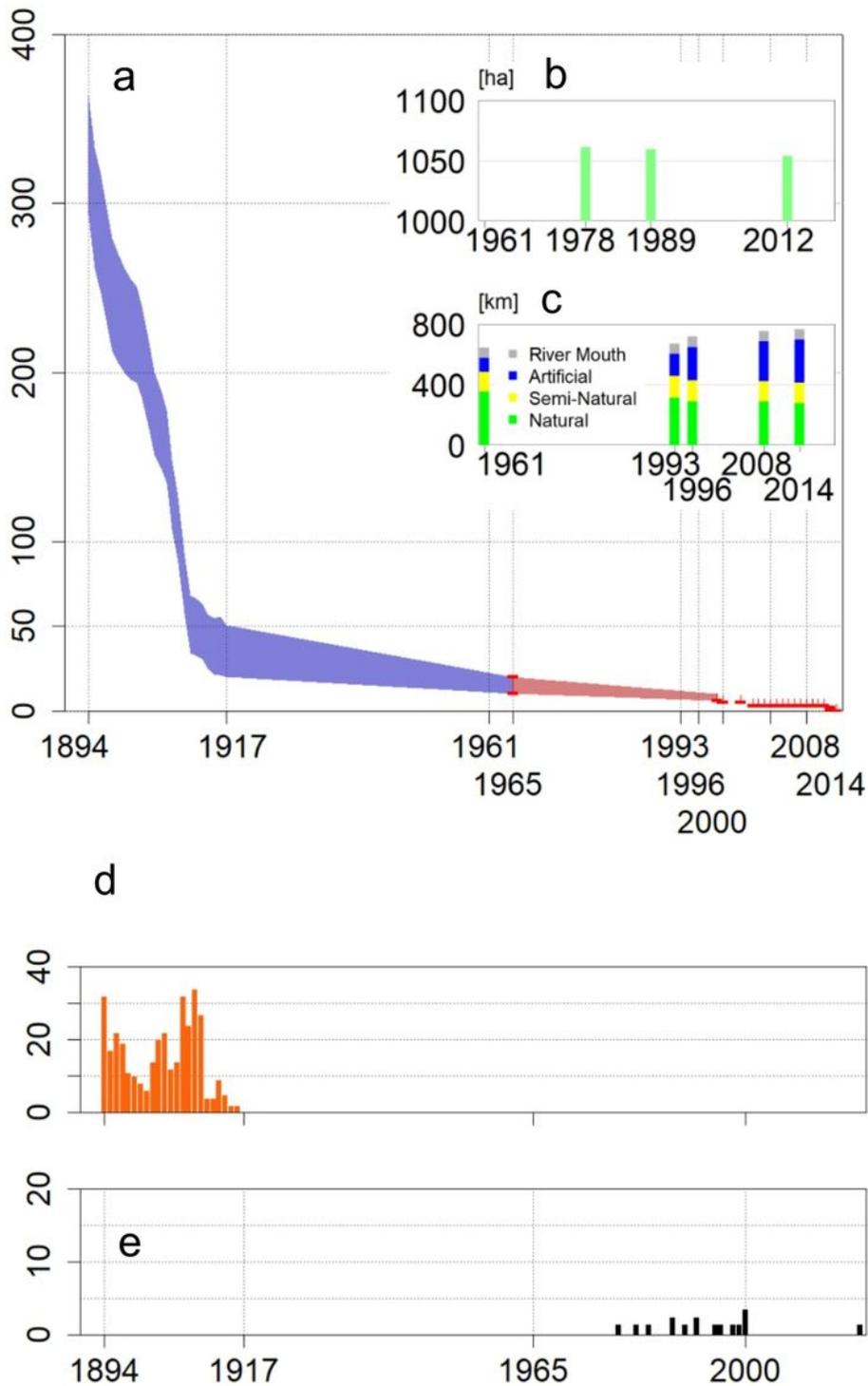
Figure 2

Time-series changes in the number of individual dugongs from 1894 to 2019. a, The estimated number of dugongs in coastal waters near the Ryukyu Islands (blue: Yaeyama, Miyako, and Okinawa Islands; red: Okinawa Island). b, Change in the area of seagrass around Okinawa Island (Extended Data Fig. 2). c, Lengths of natural (green), semi-natural (yellow), and artificial (blue) coastlines around Okinawa Island in 1961, 1993, 1996, 2008, and 2014 (Extended Data Fig. 3). d, Number of dugongs captured per year from

1894 to 1917 (Extended Data Fig. 1) (refs. 10,11). e, Records of dugong stranding or caught as bycatch since 1979.
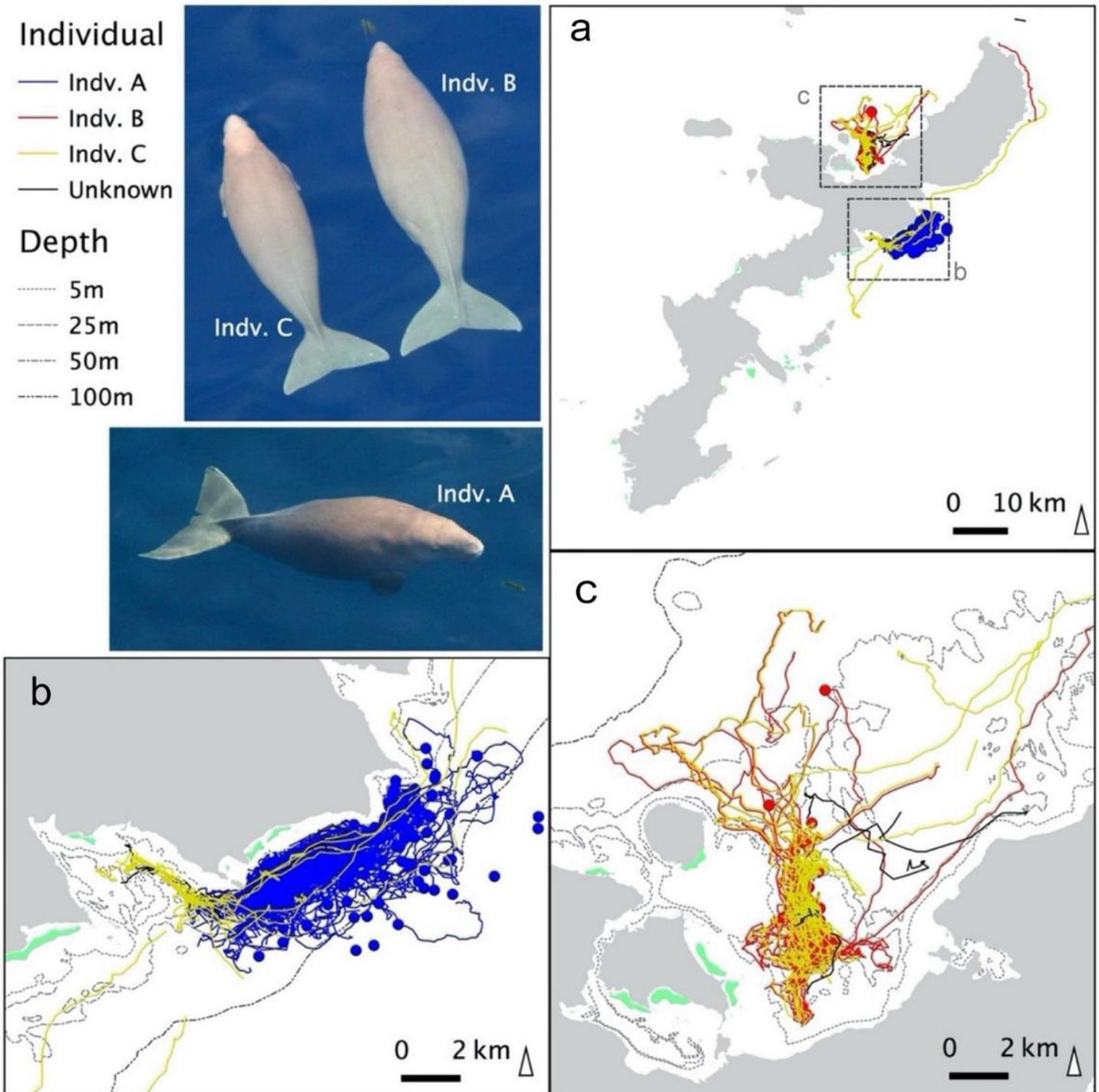

Figure 3

Tracks of the three dugongs (A, B, and C) identified since 2007. a, Tracks around Okinawa Island. b, Tracks on the coast of Kayo. c, Tracks on the eastern side of Kouri-jima and Yagaji-jima Islands.

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