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Failure in the Colonization of a New Area by Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*), Japan

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Abstract

Coastal dolphins inhabiting areas influenced by human activities can face anthropogenic threats, so monitoring surveys to detect changes in abundance are required. Photo-identification surveys of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were conducted from 2001 to 2013 in the waters south of Amakusa-Shimoshima Island, Japan, where a few dozen dolphins emigrated from the waters north of the island. We report the range, the group composition, the number of individuals, and the breeding of the dolphins settled in the new area. The dolphins were found only in narrow straits between islands. One strait was the core habitat area. Two types of groups were observed: groups with females (range of group size = 15 to 29) and those without females (range of group size = 1 to 3). The total number of dolphins gradually decreased from 31 individuals in 2001 to 18 in 2011, which was mainly attributed to the reduction in the male number from 17 to 8. Few new immigrants to the area were found. In 2009, a temporary invasion by large groups of dolphins inhabiting the northern original area occurred. After the temporary invasion started to occur, we did not observe new calves nor calves that survived to the next year. The breeding had been successful except for the first two years after the settlement. The presence of the much larger group might have negatively impacted the maternal feeding environment. It was possible that the environmental deterioration due to the red tide, which can affect fish survival, was progressing. Two females disappeared in 2011, and all the remaining dolphins disappeared in 2012. Certain dolphins were found in other areas. In the present study, the process behind the dolphins' population range expansion is examined along with factors that may have hindered the colonization process.

Key Words: new habitat, colonization, small community, invasion, photo-identification survey, Indo-Pacific bottlenose dolphins, *Tursiops aduncus*

Introduction

Long-term investigations of coastal bottlenose dolphins, genus *Tursiops*, based on individual identification have revealed the existence of subpopulations or communities which maintained relatively stable, slightly overlapping home ranges. An example is the common bottlenose dolphins (*T. truncatus*) along the west coast of Florida (Wells, 2014). Community structure exists even in a large open bay where there are few obstacles to the movement of individual dolphins (Urian et al., 2009). Communities of Indo-Pacific bottlenose dolphins (*T. aduncus*), consisting of several tens to hundreds of individuals with varying degrees of residency, have also been identified in the coastal waters, including around the oceanic islands in several regions (Kogi et al., 2004; Stensland et al., 2006; Dulau-Drouot et al., 2008; Fury & Harrison, 2008; Wiszniewski et al., 2009; Ansmann et al., 2012; Kiszka et al., 2012).

With the continuation of photo-identification surveys in each region, there has been an increase in information on identified dolphins found at locations far away from the areas at which they were originally recorded (Würsig, 1978; Wells et al., 1990; Henderson et al., 2013). In Scotland, with the expansion in the distribution of common bottlenose dolphins, identified individuals were observed in both the original core distribution area and the newly expanded area (Wilson et al., 2004; Arso Civil et al., 2019). In Japanese waters, emigration of Indo-Pacific bottlenose dolphins were found around Mikura Island as well as around Amakusa-Shimoshima Island (Nishita et al., 2015; Tsuji et al., 2017). In the Mikura Island dolphin population, approximately 15% of the 41 emigrants returned to the island waters, while some dolphins settled and reproduced in the new area. In the Amakusa-Shimoshima Island population, a few dozen dolphins settled in the new area.

Nearshore distribution makes Indo-Pacific bottlenose dolphins vulnerable to anthropogenic pressures such as the impact of bycatch and the behavioral response of the dolphins to dolphin-watching activities (Bejder et al., 2006; Kiszka et al., 2009; Reeves et al., 2013). There are concerns about the impact to the dolphins inhabiting the waters around Amakusa-Shimoshima Island (Matsuda et al., 2011; Shirakihara & Shirakihara, 2012; Inoue et al., 2017). We continued monitoring the dolphins in the new area and found that all of the dolphins disappeared unexpectedly from the area 10 y later, with some discovered in waters far away from the new area (N. Nishita, unpub. data). This indicates that the dolphins failed to colonize the new area.

Herein, we describe the range, the group composition, the number of individuals, and the breeding of the dolphins settled in the new area, and we discuss the factors that could have hindered the colonization process.

Methods

Study Area and Dolphins

The study area includes the waters around Nagashima Island (32° 10' N, 130° 10' E) which is located south of Amakusa-Shimoshima Island, western Kyushu, Japan (Figure 1). Two straits, Nagashima Strait situated between Nagashima Island and Amakusa-Shimoshima Island and Kuronoseto Strait between Nagashima Island and the mainland of Kyushu connect Yatsushiro Sound to the open sea. The north side of Amakusa-Shimoshima Island faces Tachibana Bay, which is connected to Ariake Sound by Hayasaki Strait. The maximum current velocity of the three straits reaches 7 to 8 kt/h; areas > 60 m in depth are distributed over the central part of each strait. Vast tidal flats expand in the inner areas of Ariake and Yatsushiro Sounds. There are three narrow straits between the islands east of Amakusa-Shimoshima Island which are connected to Ariake and Yatsushiro Sounds.

Photo-identification surveys initiated in 1994 revealed that year-round residents of Indo-Pacific bottlenose dolphins inhabited the waters north of Amakusa-Shimoshima Island, and its abundance was approximately 200 individuals (Shirakihara et al., 2002). An interesting feature of the dolphins is that they form a large group of more than 100 individuals and spend much time in a narrow area (Inoue et al., 2017; Nishita et al., 2017). In 2000, many of the dolphins moved to the south of the island around Nagashima Island (Nishita et al., 2015). After a year, most of the dolphins returned to the waters north of Amakusa-Shimoshima Island, but a few dozen dolphins remained. We defined the dolphins that remained in the new area as southern community (SC) members and the dolphins that returned to the original area as well as those that were only found in the original area as northern community (NC) members.

Boat-Based Surveys

Boat-based surveys around Nagashima Island were conducted between May 2001 and January 2013 (63 d; 2 to 12 d/y), mainly from spring to fall: 16 d in spring (March to May), 26 d in summer (June to August), 19 d in fall (September to November), and 2 d in winter (December to February). We used research boats belonging to Kagoshima University (*Azuma*, length 12 m, and *Hario*, length 5 m) or a chartered fishing boat. At least three research team members were engaged in a visual search for dolphins, mainly along a predetermined course.

Once a dolphin group was sighted, we followed it for photo-identification purposes. A dolphin group was defined as an aggregation that moved in the same direction and was cohesive. If the group spotted

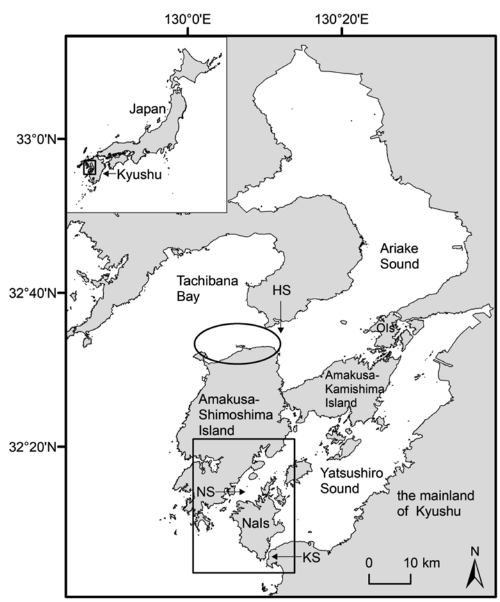

Figure 1. Study area of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Nagashima Island south of Amakusa-Shimoshima Island. NaIs = Nagashima Island, NS = Nagashima Strait, KS = Kuronoseto Strait, HS = Hayasaki Strait, OIs = Oyanoshima Island, and the oval shape = original area north of Amakusa-Shimoshima Island.

consisted of SC members, we followed it as long as possible and attempted to take photographs of the dorsal fins of all individuals in the group. Individual confirmation using binoculars was also performed by one or two researchers who were part of the team carrying out the photo-identification work for this population. Sufficient time was provided to confirm all the members of the group in most encounters. We used Canon EOS cameras (30D, 40D, 7D, or Kiss) with either a 200 or 300 mm zoom lens and 8 to 10× binoculars during the surveys. The positions of the boat were determined by GPS. All surveys were undertaken in calm conditions (Beaufort scale ≤ 3). Means of start and end times of observations of dolphin groups were 1100 and 1500 h, respectively.

Data obtained from ongoing photo-identification surveys in the waters north of Amakusa-Shimoshima Island were used to examine dolphin movements between the two study areas and the reproductive history of the females.

Range

The range of SC members was estimated by using the position data for groups consisting of SC members in the kernel analysis. We used the first position data at 3-min intervals of each group on each survey day in this analysis. The kernel density contours (50 and 95%) were generated using the *R* package 'adehabitatHR' (Calenge, 2006) with the href method of bandwidth selection.

Individual Identification, Sex Determination, Growth Stage, and Group Size

The number, shape, and position of notches on the trailing (or leading) edge of the dorsal fin were used as natural marks for identification (Würsig & Jefferson, 1990). The photographs were then matched to the photo-identification catalogue for Indo-Pacific bottlenose dolphins seen around Amakusa-Shimoshima Island since 1994.

Sex was determined based on the consistent presence of a calf and the number of years the identified individual was observed. Mean age at weaning and age at sexual maturity of males have been reported as 3.5 y and about 12 to 15 y, respectively, in other populations of Indo-Pacific bottlenose dolphins (Kogi et al., 2004; Kemper et al., 2014). Therefore, an individual that was independent of its mother at the time of the first sighting and unaccompanied by calves for 10 y or more was defined as a mature male. However, among the individuals determined to be male in the Amakusa-Shimoshima Island dolphin population, there were no individuals that were misidentified as female by the ongoing photo-identification surveys or by morphological examination after death (M. Nishita & M. Amano, unpub. data). We regarded an individual who was repeatedly observed with a calf on different days as a mature female.

A small dolphin with body size about half or less than half of that of an adult was defined as an individual who was newly born that year. The presence of fetal folds was used as an indicator of neonates. When an identifiable calf was not consistently sighted in close association with their mother, it was then regarded as having become independent.

Group size was taken as the total number of photo-identified individuals, including unidentifiable calves accompanying an identified mother. In cases for which we were able to definitely confirm the identify of dolphins visually but were not able to obtain high-quality photographs, these were included in the count to determine the group size.

Number of Individuals and Breeding

We recorded information on the breeding of the SC females. The birth season was inferred from the date on which neonates were first observed, and from the dates of the last sighting of a female without a calf and the first sighting of its new calf. In the latter case, only data in which the interval between the last and the first sightings was less than or equal to 4 mo were used. The following values on breeding were calculated following Kogi et al. (2004). The inter-birth interval (IBI) of each identified female was obtained using the number of years between births. Survival rate to the next year was calculated as N_{n1}/N_n, where N_n is the number of new calves in a given year and N_{n1} is the number of new calves that survived to the next year. Crude birth rate was calculated as N_n/N, where N is the number of all identified individuals including calves. Fecundity rate was calculated as N_{n1}/N_f, where N_f is the number of mature females. Recruitment rate was calculated as $N_{n1}/(N - N_n)$.

The rate of decrease in the number of SC members of each sex was calculated as $(N_t - N_{t+1})/N_t$, where N_t is the number of all identified individuals of each sex in a given year, and N_{t+1} is the number in the next year.

Results

Survey and Photo-Identification Effort

While boat-based surveys were carried out in the whole area around Nagashima Island, Indo-Pacific bottlenose dolphins were observed only in the Nagashima and Kuronoseto Straits (Figure 2a). The dolphins were found in all the boat-based surveys undertaken between 2001 and 2011 (58 d) but were not spotted in those between 2011 and 2013 (5 d). We spotted a total of 95 dolphin groups, and we succeeded in photographing almost all of the individuals in a group for 67 of those groups: 59 SC groups, seven NC groups, and one new dolphin. We could not take enough photographs for 28 groups, including 21 groups which contained many SC members. As for the 67 groups, the mean number of individuals photographed was 252 (SD = 363; *n* = 67).

Range

The SC groups were found in both the Nagashima and Kuronoseto Straits. The Nagashima Strait was the core habitat area as shown by the 50% kernel range (Figure 2b).

Group Composition

Two types of SC groups were found: groups with females and those without females. Size of groups with females (mean = 22.5, SD = 3.0, range = 15 to 29) was larger than those without females (mean = 1.7, SD = 0.6, range = 1 to 3). We did not find any independent calves in SC groups without females. A total of 42 SC groups with females were observed between 2001 and 2010. Each of these groups contained all the SC females who survived this period except for three groups. SC groups with females were observed every year (Figure 3).

Either a new dolphin or an NC dolphin (male, female, or individual of unknown sex) was sometimes seen in an SC group. Each was found separately. Two NC dolphins (a male and an individual of unknown sex) were first sighted in an SC group without females and were later sighted in an SC group with females before they disappeared. The time between the first discovery and the last sighting was 8 and 12 mo, respectively. The NC female and the new dolphin were sighted in an SC group with females once and 2 d in a row, respectively. The NC male and female were resighted in the original area thereafter. These four dolphins were temporary visitors.

The NC groups were first sighted in 2009 (Figure 3). The group size reached a maximum of 158 individuals (mean group size = 60.7, SD = 68.2, range = 4 to 158). Of the total of 160 NC dolphins observed in May 2009, 138 individuals (86%) had been previously observed in the original area in March 2009, and 113 individuals (71%) were resighted there in July 2009. The 12 individuals (8%) that seemed to remain in the new area until September 2009 were resighted in the original area in July 2010.

The NC group observed in May 2009 included two SC dolphins: an individual of unknown sex (#156) and a male (#249). After that, #156 and #249 were found in the original area and in the new area, respectively. The SC groups with females and the NC groups found on the same day were observed to occupy different locations and never mixed (Figure 4).

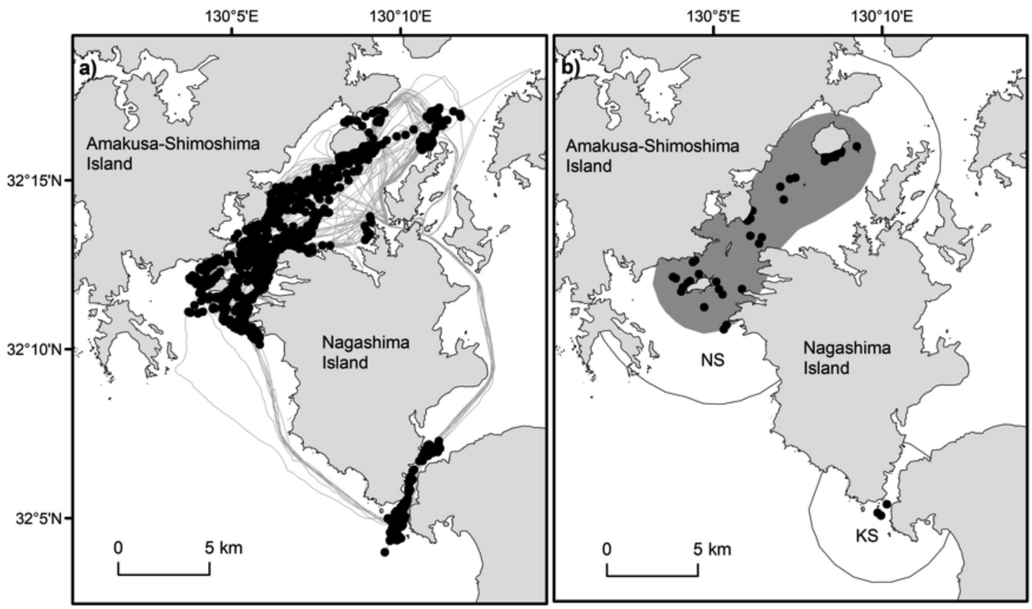

Figure 2. (a) Survey efforts (grey line) and follow points at 3-min intervals (black dot) of Indo-Pacific bottlenose dolphins around Nagashima Island, and (b) spatial distributions of SC groups shown as the 50% (dark grey area) and 95% kernel ranges, and the first sighting point of each SC group. NS = Nagashima Strait and KS = Kuronoseto Strait.

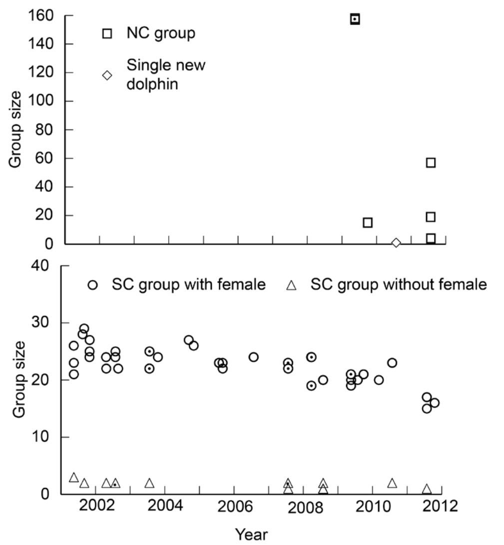

Figure 3. Group size of Indo-Pacific bottlenose dolphins around Nagashima Island. A small black dot was added to the symbol to indicate a group that contained other community members or a new dolphin.

Number of Individuals and Breeding

In May 2001, we found 30 dolphins: 17 males (eight were defined as mature males in 2003, eight in 2004, and one in 2010), seven females (including a pregnant female observed with its new calf in August of the same year), one neonate, two dependent calves (aged > 3 y and > 1 y, respectively), and three independent individuals of unknown sex. The dolphins and their offspring were defined as SC members. Note that one female with a few notches who was identified in the new area had an unknown place of origin. Sex ratio was biased towards males. The total number of SC dolphins gradually decreased to 18 individuals in 2011 (Table 1). The number of missing males varied annually. The rate of decrease in the number of SC males ranged between 0.000 and 0.214 (Table 1). There was no reduction in females between 2003 and 2009. The SC dolphins that disappeared by 2011 were not resighted in either the new or original areas except for a female who was resighted in the original area in 2002 and in 2003 (Table 2) and the individual of unknown sex (#156) mentioned above.

The calves appeared from May to September. Fetal folds were visible on four of these

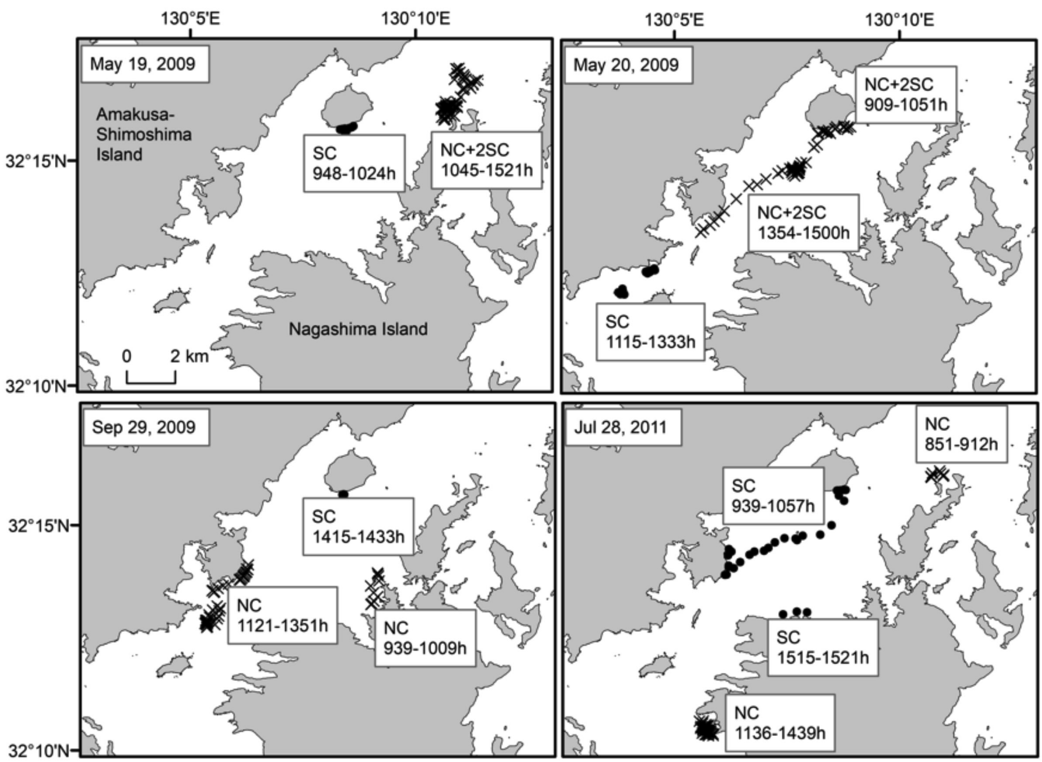

Figure 4. Follow points at 3-min intervals of two groups of Indo-Pacific bottlenose dolphins in Nagashima Strait, which were tracked alternately. The black circle = SC group with females and the cross = NC group.

Table 1. Number of individuals and demography of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of the southern community around Nagashima Island

	Year										
	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Total number of males	17	17	17	15	14	11	10	10	9	9	8
Total number of mature females (N_f)	7	6	5	5	5	7	7	7	7	7	5
Total number of immature females	2	2	2	2	2	0	0	0	0	0	0
Total number of dolphins of unknown sex including calves	5	5	3	5	3	6	6	6	6	7	5
Total number of individuals (N)	31	30	27	27	24	24	23	23	22	23	18
Rate of decrease in the number of males	0.000	0.000	0.118	0.067	0.214	0.091	0.000	0.100	0.000	0.111	
Rate of decrease in the number of females[a]	0.111	0.125	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.286	
Total number of new calves (N_n)	2	2	2	2	0	3	2	0	0	2	0
Total number of new calves that survived to the next year (N_{n1})	0	0	2	1	--	2	2	--	--	0[b]	--
Survival rate to the next year	0.000	0.000	1.000	0.500	--	0.667	1.000	--	--	0.000	--
Crude birth rate (N_n/N)	0.065	0.067	0.074	0.074	0.000	0.125	0.087	0.000	0.000	0.087	0.000
Fecundity rate (N_{n1}/N_f)	0.000	0.000	0.400	0.200	--	0.286	0.286	--	--	0.000	--
Recruitment rate ($N_{n1}/(N-N_n)$)	0.000	0.000	0.080	0.040	--	0.095	0.095	--	--	0.000	--

[a]Includes individuals who reached sexual maturity during the survey period.
[b]A calf disappeared with its mother.

individuals: one in May and three in July. Based on the dates on which the mother and calf pairs were observed, two calves were estimated to have been born between April and July and one was between May and August. The remaining eight new calves observed between July and September were considered to have been born that year.

A total of 15 new calves were observed between 2001 and 2010 (Table 2). IBI ranged from 2 to 4 y with a mean of 3.2 and mode of 3 and 4 (n = 5), excluding the birth in 2001 and in 2002. In the case of females with a calf that survived until the birth of their next calf, the IBI mean was 3.5 y (range = 3 to 4; n = 2). Calves became independent of their mothers at 2 to 3 y (2 individuals), 4 to 5 y (1 individual), 5 y (1 individual), and 7 y (1 individual).

All new calves born in 2001 and 2002 were not observed in the next year. Thereafter, the numbers of newly born calves that survived to the next year increased. We did not find new calves in the period between 2008 and 2011, except in 2010. However, the calves born in 2010 were not found in the next year. Fecundity and recruitment rates calculated for the period between 2003 and 2007 ranged from 0.200 to 0.400 and from 0.040 to 0.095, respectively (Table 1).

The breeding records of two females that disappeared in 2011 are as follows: three calves born to a female (#5000) who was identified in 2001 survived less than 2 y. We never sighted the new calf of #91 after she gave birth in the original area in 1997. The calf born at that time was #251 who gave birth in the new area in 2007 when she was 10 y old.

Discussion

The SC dolphins were geographically and socially independent of the NC dolphins, indicating that these dolphins had the characteristics of a dolphin community as defined by Wells et al. (1999). In 2009, 8 y after the SC dolphins settled in this new area, large groups of the NC dolphins invaded. They were the members of the same original community and inhabited the waters north of the

Table 2. Breeding records of females of the southern community around Nagashima Island. N = new calf including neonate, C = calf (not yearling), A = alone, S = calf who survived in the following year, M = calf with mother, SW→NW = photographed around Nagashima Island in April and in the waters north of Amakusa-Shimoshima Island in August and November, and NW = photographed in the waters north of Amakusa-Shimoshima Island. Same numeric value represents the same individual.

			Year										
ID #	Mother ID #	Identified year	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
201		1995	C_1	N&C_1^S	A	N_2	C_2	C_2	C_2	C_2	C_2	C_2	C_2^S→A
68		1994	N	A	N_3	C_3	C_3	N_4&C_3	C_4	C_4	C_4	N&C_4	C_4
158		1995	A	N	A	N	A	N_5	C_5	C_5	C_5	C_5^S	A
91		1994	C_6	C_6^S→A	A	A	A	A	A	A	A	A	
5000		2001	N	A	N_7	C_7	A	N	A	A	A	N	
28		1994	A	$A^{SW→NW}$	A^{NW}								
145		1994	A										
251	91	1997 (at birth)	M	M	A	A	A	A	N_8	C_8	C_8^S	A	A
5001	201	2001	M	M	A	A	A	A	N_9	C_9	C_9^S	A	A

island. The maximum group size of the NC dolphins reached eight times that of the SC dolphins. When the NC group appeared, the SC group with females occupied a different area from the NC group and maintained a coherent group. A similar situation was seen in 2011. Such group behavior has been observed for spinner dolphins (*Stenella longirostris*) in a remote Hawaiian atoll where resident and immigrant groups retained separate daytime resting locations (Karczmarski et al., 2005). It has been suggested that the long-term group fidelity and social stability of these spinner dolphins was facilitated by the geographical isolation and small size of the atoll. Amakusa-Shimoshima Island is small, measuring about 40 km north-south and 25 km east-west. Additionally, the distance between the original and new areas is not great. However, the dolphins need to use the narrow straits that are less than 1 km wide or the open sea to move between the two areas. The SC and NC dolphins have few chances to contact each other if the dolphins do not use these waters often. In fact, Indo-Pacific bottlenose dolphins were not found on the open sea side of Nagashima Island (Figure 2a). The geographic features may have aided in the foundation and maintenance of this new dolphin community.

The SC dolphins disappeared 10 y later, indicating that they failed to colonize the waters around Nagashima Island. Some SC dolphins were found in other areas (M. Nishita, unpub. data).

Habitat shifts of bottlenose dolphins in Shark Bay, Australia, occurred due to disturbance by the dolphin-watching industry (Bejder et al., 2006). On the north coast of Amakusa-Shimoshima Island, the dolphin-watching industry was flourishing, and behavioral changes of the dolphins were reported (Matsuda et al., 2011; Inoue et al., 2017). Therefore, the possibility that the dolphin-watching industry was one of the factors that influenced the movements of large groups from the north to the south of the island cannot be denied. Meanwhile, in Nagashima Strait, dolphin watching started in 2000 as a secondary activity to coral reef tourism which used a glass-bottomed boat. This activity was not carried out if there were no dolphins in the activity range of the tourist boat. This industry may have had some impact on the behavior of the SC dolphins, but we consider this impact to be minor.

The reduction in the number of SC males resulted in the decrease in the number of SC dolphins. Available information on dolphin deaths and emigration suggests that these may have been the cause of this reduction. Prevalence of a cutaneous nodular disease was higher in males of this population, and an SC male (#122) that disappeared was known to be affected (Van Bressem et al., 2013). Also, male bycatch may have occurred, though there is no data to support that the males are more likely to be caught accidentally than other individuals in this population. An NC male (#134) was incidentally captured by fishing gear in the waters north of Amakusa-Shimoshima Island (Shirakihara & Shirakihara, 2012). Social relationships might have also affected the reduction. In the social analyses performed when the SC dolphins lived in the original area before the community split, two SC males (#94 and #142) were clustered together with NC dolphins in a dendrogram using half-weight association index gregariousness (HWIG) values

(Nishita et al., 2015), suggesting that these dolphins had a low affinity towards other SC males. They may have left the SC because of this.

The SC females showed strong group stability in the new area, while they were not socially coherent when they lived in the original area (Nishita et al., 2015). In contrast to the disappearance of males which occurred sporadically during the 10-y survey period, female loss occurred in certain periods. Loss of two females (#91 and #5000) occurred 2 y before the disappearance of almost all SC dolphins. One female (#91) was first identified in 1994 with her neonate in the original area. During the 10-y survey period, we never saw her new calves other than her daughter (#251). These data suggest that #91 was an older female and #5000 was probably a younger female. Wells (2003) reported that a female dolphin band with long-term social relationships began to divide into a number of smaller units following an increase in numbers and loss of the oldest females. Social network studies of dolphins have shown that some females may play a crucial role in maintaining the cohesiveness of a dolphin community (Lusseau & Newman, 2004). If either or both of these females (#91 and #5000) had played an important role in the SC society, then the social stability might have been weakened.

It should be noted that we did not observe new calves or calves which survived to the next year after the invasion by NC dolphins from the original areas in 2009. Before this time, breeding was successful except for the first 2 y after the SC dolphins colonized. The fecundity and recruitment rates in the period when breeding was successful were almost within the range of the values reported for the Mikura Island population of the same species (fecundity rate: 0.121 to 0.379; recruitment rate: 0.034 to 0.121; Kogi et al., 2004). Calf survival can be affected by the condition of the calf which, in turn, is linked to maternal foraging success (Mann, 2000; Mann & Watson-Capps, 2005). The presence of the much larger NC group in the new area might have negatively impacted maternal feeding environments. In addition, the environment may have been progressively deteriorating.

In recent years, fishery damage due to red tide has become apparent in Ariake Sound, Tachibana Bay, and Yatsushiro Sound. The primary red-tide-forming organisms that affect fish survival are raphidophytes and dinoflagellates (*Chattonella* spp., *Cochlodinium polykrikoides*, *Karenia mikimotoi*, and *K. digitata*). In Yatsushiro Sound, the annual damage in 2010 reached about six times that of the average of annual damage between 1978 and 2016; in 2009, it was about three times that average, making 2010 and 2009 the highest record and the third highest record, respectively (Ministry of the Environment, 2017). Death of wild fishes, including Mugilidae, which were the dolphins' prey organisms, has been reported during the time when *Chattonella* spp. red tide occurred in the Ariake Sound (Yamazaki et al., 2008; Matsubara et al., 2009). In Florida, it has been reported that the behavior of common bottlenose dolphins was altered in association with the severe *Karenia brevis* red tides which were linked to fish mortality (McHugh et al., 2011). On the other hand, long-term site fidelity and stable abundance were reported for dolphins exposed to the *K. brevis* red tide (Bassos-Hull et al., 2013). Thus, the occurrence of red tide might have had a causal effect on the disappearance of the SC dolphins.

Insights into the range expansion process of dolphin populations are provided in the present study. The factors that hinder the colonization process are also examined.

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