## **Habitat Use by Indo-Pacific Bottlenose Dolphins (***Tursiops aduncus***) in Amakusa, Japan**

Ken Inoue,<sup>1</sup> Yumi Terashima,<sup>2</sup> Miki Shirakihara,<sup>3</sup> and Kunio Shirakihara<sup>4</sup>

*1 Okinawa Prefectural Fisheries Research and Extension Center, Kyan, Itoman, Okinawa, 901-0354, Japan*

*2 Faculty of Fisheries, Nagasaki University, Bunkyo-machi, Nagasaki 852-8521, Japan*

*3 Faculty of Science, Toho University, Funabashi, Chiba 274-8510, Japan*

*E-mail: mikishirak@me.com*

*4 Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwanoha, Kashiwa, Chiba 277-8564, Japan*

Habitat use by Indo-Pacific bottlenose dolphins Shirakihara et al., 2002; Kogi et al., 2004).<br>(*Tursiops aduncus*) with a maximum group size One of these populations inhabits the coastal (*Tursiops aduncus*) with a maximum group size > 100 individuals in the northern coastal waters waters of the Amakusa region in Kyushu, western of Amakusa-Shimoshima Island, western Kyushu, Japan (Figure 1). A photo-identification survey 1996 and December 1997. Systematic behavioral sampling and theodolite tracking techniques were (Shirakihara et al., 2002). Bycatch and dolphin-<br>used to collect data. The core habitat area (CHA), watching tourism are known to have an effect defined as the 50% kernel density estimate, was located in the northern coastal area near Tsuji reported to be greater than the potential biologi-<br>Island. Occurrences of dolphin groups in the CHA cal removal (PBR) of this population based on Island. Occurrences of dolphin groups in the CHA cal removal (PBR) of this population based on were higher during ebb and low tides. A group abundance estimated using a mark-recapture techwere higher during ebb and low tides. A group abundance estimated using a mark-recapture tech-<br>behavior that corresponded to resting was seen inque (Shirakihara & Shirakihara, 2012). Dolphinbehavior that corresponded to resting was seen around the CHA, while both traveling and feeding were seen in a wider area outside of the CHA. Dolphin groups were found in the eastern area of Dolphin groups were found in the eastern area of behavior in response to the number of boats have the CHA during morning hours, and the groups been documented (Matsuda et al., 2011). Dolphinthe CHA during morning hours, and the groups been documented (Matsuda et al., 2011). Dolphin-<br>spent more time in the CHA in the afternoon watching tourism has prospered since 1993. With hours. Unidirectional movements, mainly toward the development of the tourism industry, economic western offshore waters, occurred after 1600 h. profit increased four- to fivefold compared to Numerous dolphin-watching boats are attracted to the 1990s (Hoyt, 2001; R. Leeney, pers. comm., the CHA. Managing policies and enforcement are 20 March 2015). In 2000, the dolphin-watching the CHA. Managing policies and enforcement are 20 March 2015). In 2000, the dolphin-watching required for the local dolphin-watching industry. companies established voluntary guidelines to reg-

**Key Words:** Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, cetacean, theodolite, habitat, & Mori, 2000). However, the overall level of dolphin tourism<br>dolphin tourism<br>dolphin tourism

The Indo-Pacific bottlenose dolphin (*Tursiops* humans was recommended for *aduncus*) occurs in shallow coastal waters and (*Brownell & Funahashi, 2013*). *aduncus*) occurs in shallow coastal waters and (Brownell & Funahashi, 2013).<br>around oceanic islands in the Indian and western Land-based observations and theodolite trackaround oceanic islands in the Indian and western<br>Pacific Oceans (Hammond et al., 2012). This spe-Pacific Oceans (Hammond et al., 2012). This spe-<br>cies' nearshore distribution makes it vulnerable to<br>terms of bottlenose dolphins (*Tursiops* sp.) occurenvironmental degradation, direct exploitation, and conflicts with fisheries (Reeves et al., 2003). and conflicts with fisheries (Reeves et al., 2003). Acevedo, 1991; Harzen, 1998; Mendes et al., Genetically distinct, year-round populations of this 2002; Hastie et al., 2004; Bailey & Thompson, Genetically distinct, year-round populations of this 2002; Hastie et al., 2004; Bailey & Thompson, species have been identified in Japanese waters 2006; Photopoulou et al., 2011). In addition, use

**Abstract** (Hayano, 2013), and each population has no more than a few hundred individuals (Shinohara, 1998;

was initiated in 1994 and continues currently; the estimated abundance is around 200 individuals watching tourism are known to have an effect on this population; the annual bycatch has been watching boats offer regular trips to observe dolphing daytime hours, and changes in dolphin watching tourism has prospered since 1993. With profit increased four- to fivefold compared to companies established voluntary guidelines to regulate their actions around dolphins—for example,<br>a minimum approach distance of 30 m (Kishiro) compliance was low since boat operators did not seem to adhere to the guidelines (R. Leeney, pers. **Introduction** comm., 20 March 2015). The necessity of additional research on habitat use and interactions with

> terns of bottlenose dolphins (*Tursiops* sp.) occurring in nearshore waters (*Würsig & Würsig*, 1979; 2006; Photopoulou et al., 2011). In addition, use



**Figure 1.** Location of the study area. Closed circle = theodolite station, and triangles = observation sites where behavioral observations were conducted in addition to those at the theodolite station. The half circle shows the approximate observation range of the theodolite.

ments of dolphin behavioral changes potentially caused by vessels (Kruse, 1991; Bejder et al., caused by vessels (Kruse, 1991; Bejder et al., for dolphins and started behavioral observations 1999; Williams et al., 2002; Timmel et al., 2008; once a dolphin group was sighted. The location Matsuda et al., 2011; Lundquist et al., 2013). The advantage of this method is that dolphin behavior advantage of this method is that dolphin behavior tracking team on the hilltop via a transceiver. The (in association to boats or not) can be observed tracking team began to track the group once they without impact from research vessel presence. found it. Most often, a single large group appeared In the Amakusa region, dolphins, which are in the study area, which prompted communication seen in the northern coastal waters of Amakusa-<br>between the two teams. Surveys were conducted seen in the northern coastal waters of Amakusa-<br>Shimoshima Island throughout the year (Figure 1), for between 1 and 14 h (average  $= 6$  h) on 51 d form large groups with > 100 individuals during between 16 October 1996 and 22 December 1997.<br>daytime hours (Shirakihara et al., 2002). Dolphin Fifty-nine percent (30 d) of the surveys were condaytime hours (Shirakihara et al., 2002). Dolphin Fifty-nine percent (30 d) of the survey proups can ben observed continuously from land. ducted all day from dawn to sunset. groups can ben observed continuously from land.

The objective of this study was to reveal the Many researchers classify activities of bottle-<br>habitat use patterns of dolphins in the northern nose dolphins into categories such as traveling, olite tracking techniques. Describing the dolphins' fine-scale habitat use will help develop better-

Amakusa-Shimoshima Island, western Kyusyu, pod geometry based on distance between indi-<br>Japan (Figure 1). The island is located at the mouth viduals had a functional significance that varied with a vast tidal flat and large tidal range  $(> 6 \text{ m})$ . we recorded the following group behavioral Tachibana Bay lies on the north side of the island data by focal follow and scan sampling methods Tachibana Bay lies on the north side of the island data by focal follow and scan sampling methods and connects the sound to open water. The tidal cur-<br>(Martin & Bateson, 1986) using binoculars and a and connects the sound to open water. The tidal cur-<br>
rent (maximum speed > 13.0 km/h) in the Hayasaki field scope. We also categorized group behavior rent (maximum speed > 13.0 km/h) in the Hayasaki field scope. We also categorized group behavior<br>Strait runs in an east-west direction. According to and compared these results with dolphin activi-Matsuno et al. (1999), the current carries low salin-<br>ties reported in other waters: ity estuary waters from Hayasaki Strait toward the north, while high salinity waters are distributed **•** *Group formation* – Recorded every 3 min.<br>around Amakusa-Shimoshima Island. Three type classes were identified as (1) com-

Surveys were carried out from hilltop vantage points on Tsuji Island (40 to 46 m above sea the distance was more than five body lengths level) located north of Amakusa-Shimoshima in the other two types. In widely dispersed for-Island, and at six sites on the northeastern coast of Amakusa-Shimoshima Island (Figure 1). Three theodolite stations have been established on the *• The orientation of dorsal fins for the majority* hilltop, and we selected the most suitable for *of dolphins in group* – Recorded every 3 min. observations of dolphin groups. The search for dolphins from these hilltop vantage points by at (2) different. least four people began at dawn—one theodolite tracking team and one behavioral observation *• Duration of synchronous dives of dolphin*  team. After finding a dolphin group, we contin- *group* – Recorded whenever observed. ued to track that group until it went out of view, the sea condition worsened, or the sun set. When **•** *Surface behaviors* – Recorded whenever no dolphin groups were spotted for several tens of behaviors, no dolphin groups were spotted for several tens of

of a theodolite is broadly applicable to assess-<br>minutes, members of the behavioral observation<br>ments of dolphin behavioral changes potentially<br>team moved to one of the other six sites to search once a dolphin group was sighted. The location of a dolphin group was reported to the theodolite tracking team began to track the group once they for between 1 and 14 h (average  $= 6$  h) on 51 d

habitat use patterns of dolphins in the northern nose dolphins into categories such as traveling, coastal wastes of Amakusa-Shimoshima Island. feeding, socializing, resting, and milling based feeding, socializing, resting, and milling based We examined the core habitat area, diurnal group on their surface behaviors, direction of move-<br>behavioral patterns, and environmental factors ment, speed, and diving patterns (e.g., Shane, behavioral patterns, and environmental factors ment, speed, and diving patterns (e.g., Shane, that might affect habitat use of dolphins via sys-<br>1990). However, the present study did not use that might affect habitat use of dolphins via sys-<br>tematic behavioral sampling protocols and theod-<br>these categories because (1) detailed observathese categories because (1) detailed observa-<br>tions of surface behaviors were complicated fine-scale habitat use will help develop better-<br>informed policies for their conservation.<br> $\frac{1}{2}$  minimum number of 62 individuals (95% CI = minimum number of 62 individuals (95% CI = 48 to 76) according to photo-identification sur-**Methods** veys (Shirakihara et al., 2002), and their large distance  $(> 1 \text{ km})$  from the coast; and  $(2)$  behav-*Study Area* increases in the studies have not been previously carried out The study area included the northern coast of in this study area. Shane (1990) found that the Japan (Figure 1). The island is located at the mouth viduals had a functional significance that varied of Ariake Sound, a highly productive estuary depending on the dolphins' activity. Therefore, depending on the dolphins' activity. Therefore, and compared these results with dolphin activi-

- Three type classes were identified as  $(1)$  compact oval, (2) line, and (3) widely dispersed. *Data Collection*<br>
Surveys were carried out from hilltop vantage length in compact oval formation. Conversely,
	- of *dolphins in group* Recorded every 3 min.<br>This was divided into two types: (1) same and
	-
	-

set at hilltop vantage points on Tsuji Island (Figure 1). Group tracking was possible within to August), fall (September to November), and an approximate 5 km radius of the theodolite sta-<br>winter (December to February). an approximate 5 km radius of the theodolite stations. Vertical and horizontal angles at the most Dolphin-watching boats were frequently in the dense part of each dolphin group were saved to study area (see "Results"). To reduce the effects a laptop computer at intervals of a few seconds of boat presence, we selected the center point of a laptop computer at intervals of a few seconds of boat presence, we selected the center point of to several tens of seconds. Both angles were con-<br>a series of data collected in succession during the verted into positions (latitude and longitude), con-<br>sidering the altitude of the theodolite station mea-<br>point was an independent datum. sidering the altitude of the theodolite station measured by leveling from a triangulation point and Using a bivariate normal kernel density method, the predicted sea level at the time of each reading. with reference bandwidth as a smoothing paramethe predicted sea level at the time of each reading. with reference bandwidth as a smoothing parame-<br>The distance between the most distant individu-<br>ter for Home Range Estimation in R. Version 3.1.2 als in a group (i.e., the length of the aggregation) with the *adehabitatHR* package (Calenge, 2006), was obtained by measuring the positions of these the 50 and 95% kernel range was calculated for all was obtained by measuring the positions of these the 50 and 95% kernel range was calculated for all individuals with the theodolite. The number of position data  $(n = 268)$ . We defined the 50% kernel commercial dolphin-watching boats was recorded range as the core habitat area (CHA). In addition, every 3 min as well as the number of recreational the kernel range was estimated by season and by and research boats following the group. All sur-<br>behavioral categories which occurred frequently veys were carried out during Beaufort Sea State (B1-B5; see "Results").<br>conditions of  $\leq 3$ . We used generalized

A dataset (3-min interval) included the position of a dolphin group (latitude and longitude), behava dolphin group (latitude and longitude), behav-<br>
ioral category, frequency of occurrence of surface of dolphin groups within the CHA. Probabilities behaviors, apparent moving speed, time of day, of their presence were modeled using the factors tidal state, season, and the number of watching mentioned above as explanatory variables. The tidal state, season, and the number of watching mentioned above as explanatory variables. The boats. When theodolite angles were not recorded GLM was fitted using the maximum likelihood with a 3-min behavioral data interval, then angle technique in *R*, Version 3.1.2, and model selection readings closest to that time interval were used. followed the Akaike's Information Criteria (AIC). readings closest to that time interval were used.<br>The dolphin group behavior was classified into 12 categories on the basis of group formation (three groups among time of day and among tidal types), orientation of dorsal fins (two types), and state were examined by a Kruskal-Wallis test. types), orientation of dorsal fins (two types), and state were examined by a Kruskal-Wallis test.<br>the presence/absence of synchronous dives of the Differences in AMS and in FSB among behavioral group during the 3 min (two types). We calculated categories that occurred frequently (B1-B5; see<br>the frequency of occurrence of surface behaviors "Results") were compared with the same method the frequency of occurrence of surface behaviors "Results") were compared with the same method (FSB), excluding porpoising and fast swimming. mentioned above. In addition, Steel-Dwass All Apparent moving speed (AMS) was defined as Pairs tests (nonparametric multiple comparisons)<br>follows:<br>were used for AMS and FSB. Differences in time

T is the moving time between locations so that phin groups in the CHA using Pearson's chi-square

which were visible from land, were recorded lower values indicate a longer presence of groups and analyzed: leap, breach, head slap, body within a specific area. The time of day and tidal within a specific area. The time of day and tidal slap, and tail slap. Stationary and synchronized state were calculated as follows: the time from leaps of two or three dolphins were recorded dawn to sunset was divided into quarters—early leaps of two or three dolphins were recorded dawn to sunset was divided into quarters—early as social leaps. We did not record orientation morning (Em), late morning (Lm), early afternoon as social leaps. We did not record orientation morning  $(Em)$ , late morning  $(Lm)$ , early afternoon of the body (dorsally or ventrally). We also  $(Eq)$ , and late afternoon  $(La)$ . The longest time of the body (dorsally or ventrally). We also (Ea), and late afternoon  $(La)$ . The longest time recorded dolphins that were porpoising and was in summer (0510 to 1930 h). The time from was in summer (0510 to 1930 h). The time from fast swimming, often with constantly exposed high tide to low tide and the time from low tide to fins, which were likely indicative of fish-chas-<br>ing behavior (Shane, 1990; Hastie et al., 2004). to T4 and T5 to T8, respectively. Each symbol was to T4 and T5 to T8, respectively. Each symbol was assigned below: T1 and T8 – high tide, T2 and The position of the focal group was recorded  $T3 - ebb$  tide,  $T4$  and  $T5 - low$  tide, and  $T6$  and using a theodolite (SOKKIA DT5 or DT20ES)  $T7 - flood$  tide. Season categories were defined T7 – flood tide. Season categories were defined as follows: spring (March to May), summer (June

a series of data collected in succession during the absence of boats ( $n = 268$ ). We assumed that each

ter for Home Range Estimation in R, Version 3.1.2 position data ( $n = 268$ ). We defined the 50% kernel behavioral categories which occurred frequently

We used generalized linear models (GLM) with binomial distribution and a logit link function to *Data Analysis*<br> *A* dataset (3-min interval) included the position of factors (e.g., season, time of day, tidal state, and of dolphin groups within the CHA. Probabilities GLM was fitted using the maximum likelihood

Differences in longitudinal positions of focal Differences in AMS and in FSB among behavioral mentioned above. In addition, Steel-Dwass All were used for AMS and FSB. Differences in time of day and in tidal state were examined for pres- $AMS = D/T$  ence/absence of dolphin groups in the CHA using Pearson's chi-square test. Frequencies of occur-<br>where *D* is the straight distance between the previ-<br>ous and following locations of a focal group, and<br>compared between the presence/absence of doltest. *JMP*, Version 11.0 (SAS Institute Inc., 2013) **Results** was used for statistical analyses as well.<br>Porpoising, fast swimming, and social leaping

might give direct support to the interpretation of *Boats*<br>behavioral category, but frequencies of occur- Mean behavioral category, but frequencies of occur-<br>
Means of duration of time when no dolphin-<br>
rence of these behaviors in the dataset used  $(n \times 1)$  watching boat attended a dolphin group and durarence of these behaviors in the dataset used  $(n \times 268)$  watching boat attended a dolphin group and dura-<br>= 268) were low. Therefore, comparison of the tion of time when any dolphin-watching boat(s) frequencies of these behaviors among behavioral attended the dolphin group were 28 min  $(SD = 26)$  categories (B1-B5) was not conducted. We illus- and 44 min  $(SD = 55)$ , respectively. Mean number trated locations of the dolphin groups in which of dolphin-watching boats every 3 min increased these behaviors were observed.

# Appearance Situations of Dolphin-Watching

tion of time when any dolphin-watching boat(s) and 44 min  $(SD = 55)$ , respectively. Mean number in summer and fall and in the late morning and early afternoon (Table 1).

**Table 1.** Mean number of dolphin-watching boats (including research and recreational boats) following dolphin groups every 3 min





**Figure 2.** Spatial distribution of the 50% (inner line) and 95% (outer line) kernel ranges by four seasons

130.09 130.1 130.11 130.12 130.13 130.14 130.15 130.09 130.1 130.11 130.12 130.13 130.14 130.15 130.16 130.09 130.1 130.11 130.12 130.13 130.14 130.15 130.16 High Ebb Low Flood 130.09 130.1 130.11 130.12 130.13 130.14 130.15 130.16 Longitude Early morning Late morning Late afternoon Early afternoon  $*p < 0.0001$  $*$  p = 0.0018  $p = 0.0644$  $p = 0.1809$ 

**Figure 3.** Mean longitudes of the focal dolphin group position by tidal state and time of day; bars and dotted line indicate SE and position of the center of the theodolite station, respectively.

### *Occurrence Patterns of Dolphins*

Indo-Pacific bottlenose dolphins were tracked on all days surveyed (330 h in 51 d). In the surveys, which were conducted all day from sunrise to sunset, mean tracking time was  $8 h$  (range =  $2.5$ ) to 12.5 h). The 50% kernel range was found in the coastal area north of Tsuji Island throughout the year (Figure 2). The 95% kernel range tended to be larger in summer. The mean time of the first fixed point for confirmation of a group observation from sunrise was 99 min in spring, 46 min in summer, 133 min in fall, and 229 min in winter (Kruskal-Wallis  $\chi^2 = 9.4021$ ,  $df = 3$ ,  $p = 0.0244$ ). The ratio of observation hours (time spent tracking a dolphin group) to survey hours (time spent tracking and searching for a dolphin group) tended to increase in summer (67% in spring, 83% in summer, 72% in fall, and 58% in winter); a significant difference was detected between summer and winter (Wilcoxon test,  $p = 0.0358$ ), suggesting that dolphins are on the outside of the observation range of the theodolite from fall to spring.

The mean geographic longitude of dolphin group positions differed among the time of day: early morning (Em), late morning (Lm), early afternoon (Ea), and late afternoon (La) (Kruskal-Wallis  $\chi^2 = 61.5951$ ,  $df = 3$ ,  $p < 0.0001$ ). Dolphins were mainly seen in the coastal waters east of Tsuji Island in the morning hours. In addition, the mean longitude differed among tidal states (Kruskal-Wallis  $\chi^2 = 23.3063$ ,  $df = 3$ ,  $p < 0.0001$ ); dolphins were found in the western area during ebb and low tides. Effects of tidal states was found during the day except in LA (Figure 3).

### *Group Behavioral Categories*

Among the 12 behavioral categories, the categories of B1 through B5 accounted for 88% of the total observations when dolphin-watching boats were absent (Table 2). The frequency of each category of B1 through B5 ranged from 9.6 to 24.3%, while that of each of the other categories was 0.05 to 4.4%. Synchronous diving in a dolphin group was only seen in B1. The mean dive duration was 95 s (SD = 28,  $n = 164$ ) when dolphinwatching boats were absent. Synchronous diving tended to continue, and the mean of surface interval between dives was 87 s (SD = 38, *n* = 131). Behavioral categories of B1 and B2 had compact oval formation, B3 had line formation, and B4 and B5 had widely dispersed formation. The mean distance between the furthermost individuals in a group was 70 m  $(SD = 28)$  for the compact oval formation, 238 m  $(SD = 144)$  for the line formation, and  $542 \text{ m}$  (SD = 320) for the widely dispersed formation (Kruskal-Wallis  $\chi^2 = 34.8415$ , *df*  $= 2, p < 0.0001$ ). The orientation of dorsal fins was the same in B1 through B4 but was different in B5. Apparent moving speed (AMS) was significantly different among the behavioral categories of B1 through B5 (Kruskal-Wallis  $\chi^2 = 24.5477$ ,  $df = 4$ ,  $p < 0.0001$ ; Figure 4), and the categories B1 and B5 had lower AMS than B3 (Steel-Dwass All Pairs test,  $p < 0.05$ ). Frequency of occurrence

130.16

of surface behaviors (FSB) was significantly different among the five categories (Kruskal-Wallis  $\chi^2 = 28.1662$ ,  $df = 4$ ,  $p < 0.0001$ ; Figure 4), and behavioral category B1 had lower FSB than B2 through B5 (Steel-Dwass All Pairs test,  $p < 0.05$ ).

### *Core Habitat Area and Behavior*

The CHA was found in the coastal area north of Tsuji Island (Figure 5). The 50% kernel range of each behavioral category (B1-B5) overlapped with the CHA. However, the 50% kernel range

**Table 2.** Group behavioral category of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Amakusa, Japan  $(n = 1,755)$ 

Category	Synchronous dive	Group formation	Orientation of dorsal fins	Frequency $\%$
B <sub>1</sub>	Present	Compact oval	Same	16.2
B <sub>2</sub>	Absent	Compact oval	Same	24.3
B <sub>3</sub>	Absent	Line	Same	21.5
<b>B4</b>	Absent	Widely dispersed	Same	9.6
<b>B5</b>	Absent	Widely dispersed	Different	15.9



**Figure 4.** Means of apparent moving speed (AMS) and frequency of occurrence of surface behaviors (FSB) in each of the five behavioral categories (B1-B5); bars indicate SE.

of B1 and B5 were narrower than that of the CHA. In contrast, the 50% range of B2 through B4 was wider than the CHA. The GLM showed that dolphin occurrences within the CHA could be explained by the tidal state and time of day (Table 3). Dolphins were found within the CHA in the early and late afternoons (Pearson's  $\chi^2$  = 27.384, *p* < 0.0001; Figure 6). Dolphins were seen within the CHA during ebb and low tides but outside the CHA at high and flood tides (Pearson's  $\chi^2$  = 64.189, *p* < 0.0001; Figure 6). Behavioral categories and inside/outside the CHA was not independent (Pearson's  $\chi^2 = 23.551$ ,  $p < 0.0001$ ; Figure 7). Behavioral category B1 showed the highest frequency (28%) of dolphins observed within the CHA. In contrast, 68% of observations outside the CHA were associated with behavioral categories B2  $(31\%)$  and B3  $(37\%)$ .

Social leaps were seen more often in the northern waters of Tsuji Island, whereas porpoising and fast swimming were seen over wider areas, including the coastal areas of the west and east side of the island (Figure 8). A focal group frequently moved in one direction (mainly offshore to the west) in the afternoon after 1600 h (Figure 8); this was observed in 57% of the surveys, which wereconducted all day from dawn to sunset  $(n = 30)$ .

### **Discussion**

Indo-Pacific bottlenose dolphins were observed in the northern waters of Amakusa-Shimoshima Island, western Kyushu, Japan, throughout the year. The CHA was located in the coastal area north of Tsuji Island, where dolphins spent much of their time daily. Distribution of bottlenose dolphins, *Tursiops* sp., has been examined in aerial and ship surveys, which were conducted over a wide range of Ariake Sound and Tachibana Bay (Shirakihara et al., 1994; Yoshida et al., 1997; Shirakihara & Shirakihara, 2012). The results indicated that there were only a few sightings of *Tursiops* sp. except for in the northern waters of Amakusa-Shimoshima Island. We concluded that the waters north of Amakusa-Shimoshima Island, especially the coastal area north of Tsuji Island, are important habitat for this dolphin population.

In the present study, five behavioral categories (B1-B5) were recognized (Table 2). We compared these categories with dolphin activities reported in other waters (Shane, 1990; Lusseau, 2003; Mann & Watson-Capps, 2005; Stensland et al., 2006; Steiner, 2012; Karniski et al., 2015) and reclassified our behavioral categories to these dolphin activities. Behavioral category B1 with its low AMS and very low FSB had similar characteristics to the activity known as resting. Behavioral categories B2 and B3 had a high AMS, suggesting that



**Figure 5.** Spatial distribution of the 50% (inner line) and 95% (outer line) kernel ranges; dark gray shows core habitat area (CHA). The behavioral categories of B1 through B5 are defined in Table 2.

the group did not stay in one region. Their 50% of kernel ranges were wide. We considered these categories to resemble the activity known as traveling. Behavioral category B4 may occur at the starting time of feeding behavior; we have seen that dolphins milled in various locations after they moved rapidly in a dispersed formation. Similar behaviors have been reported for bottlenose dolphins in Argentina and South Africa (Saayman et al., 1973; Würsig & Würsig, 1979). Behavioral category B5 had the lowest AMS and the highest FSB. According to previous studies, FSB and no forward movement were characteristics of the behavior known as socializing; thus, B5 was somewhat similar, but behavioral category B5 may include feeding behavior as well.

We compared frequency of occurrence of each behavioral category (B1 corresponds to resting, 16%; B2 and B3 correspond to traveling, 46%; and B4 and B5 correspond to feeding or socializing, 26%) to the activity budget of Indo-Pacific bottlenose dolphins reported elsewhere: 9 to 34% for resting, 20 to 61% for traveling, and 32 to 66% for feeding or socializing (Möller & Harcourt, 1998; Chilvers et al., 2003; Mann & Watson-Capps, 2005; Stensland et al., 2006; Steiner, 2012). Frequency of occurrences of B1 through B3 (corresponding

**Table 3.** Evaluation of factors affecting occurrence within the CHA (estimated by 50% kernel density estimate) using Akaike's Information Criteria (AIC) of generalized linear models (GLMs) with explanatory variables. The symbol (\*) shows the lowest AIC.

Explanatory variables	AIC
Tidal state $+$ Time of day	385.9*
Tidal state $\times$ Time of day	388.0
Tidal state $+$ Time of day $+$ Behavior	388.7



**Figure 6.** Frequency of occurrences of the focal dolphin group inside and outside of the CHA (estimated using the 50% kernel density) by time of day and tidal state. Sample numbers:  $n = 151$  for inside of the CHA, and  $n = 117$ for outside of the CHA. Em  $=$  early morning, Lm  $=$  late morning,  $E_a =$  early afternoon, and  $La =$  late afternoon.



**Figure 7.** Frequency of occurrences of behavioral categories inside and outside of the CHA (estimated using the 50% kernel density). Sample numbers:  $n = 151$  for inside of the CHA, and  $n = 117$  for outside of the CHA.

to resting and traveling) was within the range of previous findings, but those of B4 and B5 (feeding or socializing) were below the range. This trend might be attributed to differences in survey methods and behavioral definitions (Steiner, 2011; Karniski et al., 2015). Feeding behavior might have been included in the other categories in Table 2; however, dolphins may have other feeding areas outside the study area, or dolphins may feed more actively at night.

There is a possibility that dolphins use a wider area beyond the study area at night. Most of the daily first sightings were located in the coastal area east of Tsuji Island. Often, a dolphin group moving in the direction of Tsuji Island was seen in the morning, suggesting that dolphins came from the Ariake Sound. In contrast, in the afternoon, movements offshore to the west were frequently observed. This pattern resembles the behavior of Hawaiian spinner dolphins (*Stenella longirostris*), which entered the bay in the early morning and departed in the late afternoon for nighttime feeding in deep waters (Norris et al., 1994). Most of our study area is shallow  $( $30 \text{ m}$ ), but there$ is a deep sea area (> 60 m) between Shimabara Peninsula and Amakusa-Shimoshima Island, and near the middle of Ariake Sound (Figure 1). Bycatch of Indo-Pacific bottlenose dolphins and possible depredation of dolphins were reported in the central waters on the east coast of Tachibana Bay and in the middle waters of Ariake Sound (Shirakihara & Shirakihara, 2012). To clarify whether Amakusa dolphins hunt prey over wider areas at night, introduction of various research techniques, such as biologging techniques, including satellite tracking to this study area, would be required. Research using stationed acoustic buoys clarified some nocturnal behavior of the Indo-Pacific bottlenose dolphins around Mikura Island, Japan (Morisaka et al., 2015).

Porpoising and first swimming, and B4, which may suggest feeding, were seen in the wide area, including the outside of the CHA, suggesting multiple feeding areas exist in the northern coastal waters of Amakusa-Shimoshima Island. Dolphins preferred to stay in the CHA during ebb and low tides. According to the Marine Cadastre by the Japanese Coast Guard (www1.kaiho.mlit.go.jp/ KAN10/kaisyo/tidal\_c/index.htm), at ebb tide, the tidal current is predicted to flow toward the west in the coastal area east of Tsuji Island, near Hayasaki Strait, while it flows toward the east in the coastal area west of the island, near Tomioka Bay (Figure 1). At flood tide, the currents run eastward in both the east and west side of the island (i.e., the tide flows in the same direction). The longer time Amakusa dolphins spent within the CHA during ebb and low tides may be related to this complex flow pattern of tidal currents. The tidal current may provide feeding areas around Tsuji Island, especially during the ebb and low tide. Tidal effects on bottlenose dolphin movements, activities, and area use have been studied worldwide (e.g., Würsig, 1978). In the inner Moray Firth, dolphin sightings were most frequent during flood tide (Mendes et al., 2002). In contrast, in the outer estuary of the River Shannon, the sighting peaked during ebb tide (Berrow et al., 1996). These surveys were carried



**Figure 8.** Locations of dolphin groups where porpoising, first swimming, and social leaping were observed, and where evening movements occurred after 1600 h

out from land. In a boat-based sighting survey for Indo-Pacific bottlenose dolphins in the Clarence River estuary, sightings peaked during flood tide, and dolphins were widely dispersed during high and flood tides rather than during low and ebb tides, possibly in response to prey distribution, temperature, risk of stranding, and habitat accessibility (Fury & Harrison, 2011).

Although this research was carried out in the late 1990s, ongoing research in the region confirms that a large group of dolphins is still present, and these dolphins are the focus of a large dolphin-watching industry (R. Leeney, pers. comm., 20 March 2015; M. Nishita, pers. comm., 20 March 2015). Numerous dolphin-watching boats are attracted by the CHA, but there are no official regulations for their activity in Amakusa.

The B1 category, which corresponds to rest, was the most frequently observed behavioral category in the CHA. The CHA is considered to be an important resting area for the population. Lusseau (2003) revealed that the resting behavior was sensitive to boat interactions. In Amakusa, the effects of the presence of dolphin-watching boats on the behavioral category B1 were detected—namely, an increasing number of boats led to longer diving times, higher moving speed at the surface, larger distances from diving to subsequent surfacing positions, and shorter inter-diving intervals (Matsuda et al., 2011). The dolphins are vulnerable to dolphin-watching activity.

Given the intrusive nature and the frequency of dolphin-watching activities around Amakusa, which focuses solely on this population, the importance of the industry to the local economy, and also the known negative impacts of irresponsible cetacean-watching activities on wildlife, it is essential that this industry is better managed. Management actions should include a limit on the number of boats approaching a dolphin group and the amount of time that any vessel may spend with dolphins within a 24-h period. In Japan, there are dolphin-swimming locations where a limitation on the number of boats has been introduced (Mori, 2005; Kogi, 2009). Though voluntary, such self-imposed regulations are strongly recommended for managing dolphin-watching activities in the coastal area north of Tsuji Island. Our results related to habitat use by dolphins in the region support the development of dolphinwatching regulations.

### **Acknowledgments**

We would like to thank Megumi Kuroda (Takatsuki), Noriko Matsuda (Shirao), Masataka Kanda, and Ryuji Iwai for assistance with fieldwork; Yasushi Hirayama who kindly lent us a theodolite and taught us how to use it; Taiji Harada, Motoi Yoshioka, Syoichi Kita, and Toshio Kasuya for useful suggestions; and Hiroto Murase for helpful suggestions on GIS techniques. We are grateful to Masao Amano and Ruth H. Leeney for valuable suggestions and comments. We also would like to thank the editor, Kathleen M. Dudzinski, and the anonymous reviewers for helpful comments.

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