Aquatic Mammals 2020, *46*(6), 531-541, DOI 10.1578/AM.46.6.2020.531

Prey Species and Foraging Behaviour of Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) Around Mikura Island in Japan

Rikiya Takahashi,[1] Mai Sakai,[1] Kazunobu Kogi,[2] Tadamichi Morisaka,[3] Takao Segawa,[3] and Hiroshi Ohizumi[4]

[1]*Department of Fisheries, Kindai University, 3327-204 Nakamachi, Nara 631-8505, Japan*
E-mail: sakaimai@nara.kindai.ac.jp
[2]*Mikura Island Tourist Information Centre, Mikurajima-mura, Tokyo 100-1301, Japan*
[3]*Cetacean Research Center, Graduate School of Bioresources, Mie University, 1577 Kurimamachiya-cho, Tsu, Mie 514-8507, Japan*
[4]*Department of Marine Science and Technology, Tokai University, 3-20-1 Orido, Shimizu, Shizuoka 424-8610, Japan*

Abstract

This study aimed to assess the prey species and foraging behaviour of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, a small oceanic island ~200 km south of Tokyo, Japan, using underwater observations and stomach content analysis of eight individuals to determine the feeding ecology of this population. Our results suggest that *T. aduncus* feed on various species and exhibit concentrated foraging behaviour at night. We recorded 11 fish species, seven cephalopod species, and one crustacean species as prey, as well as 10 fish species and one crustacean species as potential prey. Our underwater observations revealed that females performed foraging behaviour during daytime significantly more frequently than males. This is the first study using underwater observations to assess foraging and prey species of small cetaceans in Japan.

Key Words: diet, observation, stomach contents, mesopelagic, neritic, epipelagic, night-time feeding, female bias

Introduction

It is important to study the feeding ecology of marine mammals to understand their habitat and life history (Amir et al., 2005; Trites & Spitz, 2018). The habitats of cetaceans are linked to those of their prey species (Irvine et al., 1981; Hanson & Defran, 1993; Vaughn et al., 2010; Bouveroux et al., 2018). For example, it has been documented that bottlenose dolphins (*Tursiops truncatus*) extended their range northwards from the California coastline in response to changes in prey distribution related to the 1982-1983 El Niño event (Hanson & Defran, 1993).

Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are distributed in shallow coastal waters from South Africa and across the Indian Ocean to Southeast Asia and Australia (Wang, 2018). Previous studies have suggested that *T. aduncus* feed on various fish and cephalopod species that are abundant in specific regions (Amir et al., 2005; Yamazaki et al., 2008; Mizrahi et al., 2009; Kiszka et al., 2014; Ansmann et al., 2015; Table 1). The geographical environment of previous studies mostly included coastal areas of the mainland with a sandy or reef bottom.

One hundred and sixty Indo-Pacific bottlenose dolphins were seen around Mikura Island, Tokyo, Japan (Connor et al., 2019). Mikura Island exhibits different environments. It is a small oceanic island about 200 km away from the mainland, and it harbours no bays, provides easy access to the deep sea (because of steep slopes around the island; Figure 1), and consists of a rocky base (Nakasuji, 2012). These variations in habitat suggest that the feeding habits of this population are unlikely to be the same as known behaviours reported previously. However, there are currently no in-depth studies on the foraging behaviour and feeding time or location for this population.

Prey species of small cetaceans can be analysed using four methods: (1) stable isotopes, (2) stomach contents, (3) mtDNA of feces, and (4) direct observation; however, there are differences in detectability among all methods (Jansen et al., 2013; Kiszka et al., 2014; Ansmann et al., 2015). Therefore, the combination of these methods enables a more rigorous assessment. Researchers are not permitted to conduct invasive sampling (e.g., biopsy),

Table 1. Summary of previous studies on prey species of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)

Study site	Habitat	Method	Prey	Number of individuals	Reference
Zanzibar, Tanzania	Coastal area with a sandy or soft coral base	Stomach contents	Fifty fish species (including *Apogon apogonides*, *Lethrinus crocineus*, *Lutjanus fulvus, Synaphobranchus kaupii*, and *Uroconger lepturus*) and three squid species (*Loligo duvauceli*, *Sepia latimanus*, and *Sepioteuthis lessoniana*)	26	Amir et al., 2005
Mayotte, France (northeast of the Mozambique Channel)	Epipelagic and demersal areas with a reef base	Stable isotope and behavioural observations	Six fish species (*Caranx melampygus*, *Mugil cephalus*, *Mulloidichthys vanicolensis*, *Scarus russeli*, *Siganus argenteus*, and *Tylosurus crocodilus*)	28	Kiszka et al., 2014
Amakusa, Japan	Mouth of the bay, rivers, and a large tidal area	Stomach contents	Five fish species (Congridae, *Ilisha elongata*, Mugilidae, *Chelon* sp., and Monacanthidae) and one squid species (*Loligo* sp.)	1	Yamazaki et al., 2008
Mikura Island, Japan	Oceanic island with a rocky base	Stomach contents	Two fish species (*Cypselurus agoo* and *Parexocoetus mento*), four squid species (*Todarodes pacificus*, *Enoploteuthis chunii*, *Onychoteuthis borealijaponica*, and Cranchiidae), and one crustacean species (*Albunea symnista*)	2	Kakuda et al., 2002
		mtDNA	Seventy-four fish species (including *Polymixia japonica*, *Beryx splendens*, *Emmelichthys schlegelii*, *Ariomma lurida*, and *Scomber australasicus*) and 11 cephalopod species (including *Todarodes pacificus*, *Loligo oualaniensis*, *Eucleoteuthis luminosa*, *Loligo edulis*, and *Ommastrephes bartramii*)	166	Kita et al., 2018

however, due to dolphin conservation laws around Mikura Island (Local Rule, Mikura Island Tourist Information Centre [MITC]). Two previous studies on prey species of *T. aduncus* have been performed using analyses of stomach contents and mtDNA (Kakuda et al., 2002; Kita et al., 2018; Table 1). However, the stomach contents were sampled from only two entangled individuals (Kakuda et al., 2002). Moreover, Kita et al. (2018) reported that there were certain contaminations in the analysis. Furthermore, caution is warranted when conducting mtDNA analysis considering the risk of detecting secondary prey species. On the other hand, Mikura Island is a suitable environment for underwater observation; therefore, many studies on social behaviours and interactions have been conducted there (Dudzinski et al., 2010; Sakai et al., 2010, 2016). However, this is the first study to employ direct underwater observation of foraging behaviour.

In addition, individual identification of dolphins based on sex, age, and kinship (using underwater video recordings) has been underway since 1994 (Connor et al., 2019). Collection of such data (including sex, age, and kinship of each individual) allows for comprehensive analysis of the observed behaviours. This information is crucial because prey species and foraging behaviour may differ depending on age class and/or sex. Previous studies showed that females tend to forage during daytime more frequently than males (Barros & Wells, 1998; Sprogis et al., 2016, 2017). Moreover, the foraging dive duration of females varies in response to the age and sex of their calves such that females showed prolonged dive duration as their calves get older (Miketa et al., 2018).

The aim of the present study was to assess the prey species and foraging behaviour of *T. aduncus* using underwater observation in Mikura Island, Japan. We also analysed the stomach contents of eight wild Indo-Pacific bottlenose dolphins stranded around the island in the past 20 years.

Methods

Study Area and Population

Mikura Island is located ~200 km south of Tokyo, Japan (33° 52' N, 139° 36' E; Figure 1). It has a circumference of 16.4 km and an area of 20.58 km^2.

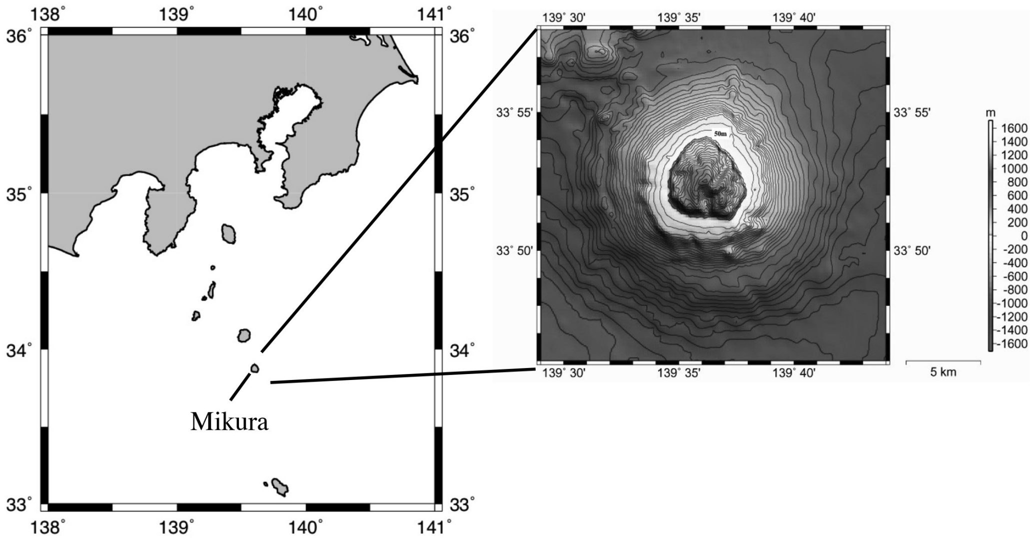

Figure 1. Location of Mikura Island, Japan (*Source:* Japan Coast Guard website: https://www1.kaiho.mlit.go.jp/GIJUTSUKOKUSAI/kaiikiDB/kaiyo11-2.htm)

The ocean floor is mostly boulder-strewn, and it is composed of seaweed in parts (Nakasuji, 2012). Depth ranges from ~2 to 45 m within 300 m from the shore.

A pod of 160 Indo-Pacific bottlenose dolphins is distributed around Mikura Island (Kogi et al., 2004). Identification using underwater video recordings of individuals' natural marks (e.g., scars, cookie cutter shark bites, and/or notches on fins) has been conducted yearly from May to October since 1994 to date (Connor et al., 2019). The male/female ratio of the identified individuals is 1.00/1.03 and has remained nearly the same from 1994 to 2019 (MITC, unpub. data).

Definition of Foraging Behaviour and Identification of Prey Species

In the present study, the definition of foraging behaviour follows Bender et al. (2009) and Barros & Wells (1998). Eat (code E) is the state in which the dolphin swallowed an organism (Bender et al., 2009). We defined organisms that corresponded to code E as prey species. Bite (code B) is the state in which the dolphin bit and kept an organism in its beak but did not swallow (Barros & Wells, 1998). Organisms that corresponded to code B were referred to as potential prey species and represent cases where a dolphin bit and kept some organisms like fish in their mouths, playing and developing their foraging skills (Samarra et al., 2018), or when a dolphin tapped on the water surface and swung while biting an organism to make digestion easier (Smith & Sprogis, 2016; Sprogis et al., 2017). The observed prey species were identified using the features of their appearance in video footage.

Analysis of Identification Research Video

We analysed foraging behaviour and prey species using video data obtained for identification research from May to October 2015, June to October 2016, and June to October 2017 for 183 d and across 318 surveys (total of 107.3 h). Field research was conducted while riding on a dolphin-watching tour boat for ~2 h per survey, mainly between 0800 and 1600 h (local time). The survey was conducted when wave height was less than ~2 m. The water was generally clear, with visibility up to approximately 30 m. Handheld video cameras (HDR-CX430V and HDR-XR550V; Sony, Tokyo, Japan) set in waterproof housings (Seatool/Recsea; NTF, Kanagawa, Japan) were used.

We recorded all fish and cephalopod species that were potential prey, time of the sightings, and whether physical contact occurred between them and the dolphins in the video. The distance between the dolphin and the observer ranged from 3 to 30 m.

Collection of Information from the Public

We collected the video and photographs of foraging behaviour from tourists and guides of dolphin-watching tours from April 2018 to March 2019. An online input form was created using the free customer support tool "Tayori" (PR TIMES, Inc., Tokyo, Japan); it was offered to the tourists and guides at random for cooperation on the website and social networking service (SNS). As a result, eight tourists and eight guides reported 39 cases of information through the web forms and SNS. These 39 cases included photographs (n = 19) or videos (n = 20; 1,011 s). The date and time of observation as well as the sex and age of the foraging individual, target prey species, and the foraging behaviour code (B or E) were identified by the first author (RT) based on their morphology and natural marks using photographs or video footage.

Analysis of Foraging Individuals

The time of foraging behaviour, ID number, age class, sex, and reproductive state of each foraging individual from 50 episodes of foraging behaviour (ID research video [n = 11] and videos and photographs from the public [n = 39]) were recorded by referencing the ID research data. The definition of each age class in this study followed that of Kogi et al. (2004). To assess the foraging probabilities, binominal tests (two-tailed) were conducted by taking the total recording time of each sex as a population ratio.

Interview Research

The authors performed interview research on prey species and foraging behaviour and selected interviewees at random from the dolphin-watching tourist guides and boat captains who had licenses as official Tokyo nature guides. Interviews were conducted from 3 to 9 October 2018, and answers were obtained from 23 licensed guides (seven captains and 16 guides). The first author (RT) asked the interviewees two questions. The first was "What was their approximate number of sightings of *T. aduncus* foraging behaviour per year?" The answer was multiple choice: 0-10 times, 11-20 times, 21-30 times, or over 30 times. The second question was "Is the prey species that they had observed ever based on their experience?" We excluded the species that were reported by other methods (e.g., collecting information from the public) to prevent data duplication. All species mentioned in these interviews were deemed as potential prey species because these results comprised only the experiences and memories of the interviewees.

Records of Stomach Contents and Regurgitated Prey

Fishermen caught 10 individuals as bycatch from 1996 to 2017 off Mikura Island (MTIC, unpub. data), and Kakuda et al. (2002) analysed the stomach contents of two of these individuals. A co-author (KK) necropsied another eight individuals and collected their stomach contents. The stomach contents of two individuals had no records (were empty), and those of five other individuals were almost undigested. The undigested samples were identified by KK with reference to Nakabou (2000) using external morphology such as the number of fin rays. The stomach contents of the last individual (stranded on 25 June 2008) were frozen and sent to another co-author (HO). The stomach contents of this sample were thawed and weighed, and then the semi-digested fish were removed. Fish that could be identified based on their external morphology were also identified by referencing Nakabou (2000) using the number of fin rays. If the fish species could not be identified from external morphology, the sagittal otolith was removed and identified. Subsequently, the jaw plate, bone, and flesh were removed. Otoliths and jaw plates were identified using the appropriate references (Ohe, 1985; Clarke, 1986; Rivaton & Bourret, 1999; Kubodera, 2005).

We used two different indices to investigate the occurrence and relative importance of the prey found in the stomachs (Amir et al., 2005), and we calculated the percentage by number (%N) and percentage frequency of occurrence (%FO) using the following formulae:

$$\%N = (\text{amount of a single species in all stomachs/total amount of all species in all stomachs}) \times 100$$

$$\%FO = (\text{number of dolphins in which species was found/total amount of dolphins}) \times 100$$

All organisms recorded in the stomach contents were defined as prey species, and these results were compared to the observation results.

A dolphin-watching guide provided us with part of a squid regurgitated by a dolphin, which was identified by one of the authors (TS) using 16S ribosomal RNA (16S rRNA) and cytochrome b (Cytb) sequences, a widely used technique for genetic identification (Chin et al., 2016; Wen et al., 2017). The genomic DNA was extracted from a 25 mg piece of muscle tissue, and amplification and sequence analysis were performed as described previously by Ohtsuka et al. (2018). The species was identified by BLAST search (Altschul et al., 1990).

Results

Analysis of Identification Research Video

We fitted all 11 cases that confirmed dolphin contact with organisms to a definition of foraging behaviour (E: Eat [code E] was the state in which the dolphin swallowed an organism and B: Bite [code B] was the state in which the dolphin bit and kept an organism in its beak but did not swallow). In one unclear case of *Labracoglossa argenteiventris*, we decided to use code E because a co-author (TM) directly observed a dolphin swallow this species at that time. In 10 cases of foraging behaviour confirmed as code B, only three cases of *Prionurus scalprum* (*n* = 2) and Exocoetidae (*n* = 1) could be identified.

Collection of Information from the Public
Thirty-nine cases were classified to a definition of foraging behaviour (codes E or B). The most frequently reported case was *Octopus* sp. (*n* = 13). Three species (*Octopus* sp., Exocoetidae [*n* = 5], and *P. scalprum* [*n* = 4]) were classified as code E and confirmed as prey species. Four species (Muraenidae [*n* = 3], Belonidae [*n* = 2], *Parajulis poecilepterus* [*n* = 1], and *Myrichthys maculosus* [*n* = 1]) were classified as code B and confirmed as potential prey species. The other 10 cases could not be identified.

Analysis of Foraging Individuals
All foraging behaviours (*N* = 50) from identification research video data (*n* = 11) and information collected from the public (*n* = 39) were analysed. Dolphins feed on one prey item per feeding event and did not demonstrate any group hunting.

In 43 cases out of 50, the sex of foraging individuals was identified. Foraging probabilities were significantly higher for females (*n* = 39) than for males (*n* = 4) when the total recording time of each sex was taken as a population ratio (female:male = 200,385:124,953 s, binomial test, two-tailed, $p < 0.01$; Figure 2). Eleven females were observed with their calves, and five were considered pregnant. These data were confirmed the following year when births were identified using the identification research data.

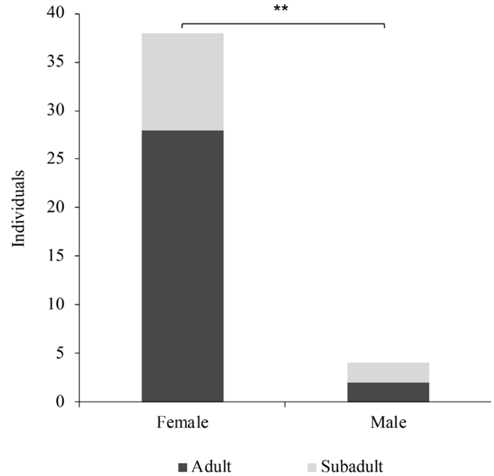

Figure 2. Number of foraging individuals in each sex and age class (*n* = 43, binomial test, two-tailed, $**p < 0.01$)

Interview Research
The information from the interviewees and the number of foraging behaviours observed are listed in Table 2. Seventy-four percent of the

Table 2. Number of foraging behaviours observed during the interviewees' career. The figure in each cell indicates the number of persons.

Career (years)	Frequency (Number of sighting times of foraging behaviour/year)			
	0-10	11-20	21-30	>30
1	3	0	1	0
2	3	0	0	0
3	2	0	0	0
4	1	0	1	0
7	1	0	0	0
8	1	0	1	0
10	1	0	0	0
11	0	0	0	1
12	0	0	0	1
13	2	0	0	0
14	0	0	1	0
15	1	0	0	0
20	1	0	0	0
26	1	0	0	0
Total	17	0	4	2

Table 3. Stomach content records of *T. aduncus* stranded during 1996 to 2017; %N = percentage number and %FO = percentage of frequency.

Date	ID code	Sex	Age (year)	Prey species	Number of preys	%N	%FO	Cause of death
26 May 1996	#026	F	--	*Cypselurus agoo*	7	9%	12.5%	Unknown (Kakuda et al., 2002)
20 July 2001	--	M	--	*Albunea symnista*	Several	--	12.5%	Unknown (Kakuda et al., 2002)
				Parexocoetus mento	2 head and 2 postcranial	5%	12.5%	
				Todarodes pacificus	2	3%	12.5%	
				Enoploteuthis chunii	2	3%	12.5%	
				Onychoteuthis borealijaponica	1	1%	12.5%	
				Cranchiidae	3	4%	12.5%	
10 July 2005	--	F	--	No record	--	--	--	Entangled in gillnet
11 June 2008	--	F	--	No content	0	--	--	Unknown
25 June 2008	#165	M	13	*Decapterus* sp.	11	14%	12.5%	Entangled in gillnet
				Scomber australasicus	9	11%	12.5%	
				Serranidae	1	1%	12.5%	
				Nealotus tripes	1	1%	12.5%	
				Beryx splendens	1	1%	12.5%	
				Eucleoteuthis luminosa	1	1%	12.5%	
				Unidentified fish	1	1%	12.5%	
25 July 2008	#259	M	12	*Labracoglossa argenteiventris*	4	35%	50%	Entangled in gillnet
				Pempheridae sp.	4	5%	12.5%	
7 June 2011	#454	M	9	*L. argenteiventris*	15	--	--	Entangled in gillnet
				Scomber sp.	2	3%	12.5%	
				Decapodiformes	2	3%	12.5%	
25 May 2012	#356	F	13	*L. argenteiventris*	4	--	--	Entangled in gillnet
16 June 2013	#406	M	14	*L. argenteiventris*	5	--	--	Entangled in gillnet
16 July 2017	#626	M	4	Unidentified fish	--	--	--	Entangled in gillnet

interviewees ($n = 17$) answered that they saw foraging behaviours only 1 to 10 times per year; the rest of the interviewees observed it 11 to 20 times ($n = 4$) or over 30 times ($n = 2$). *Calotomus* sp., Decapoda, *Hyperoglyphe* sp., *Hyporhamphus* sp., *Katsuwonus* sp., Labridae, and *Spratelloides* sp. were reported as potential prey.

Records of Stomach Contents and Regurgitated Prey

We confirmed 10 fish species, five cephalopod species, and one crustacean species from the stomach contents of eight individuals (Table 3). The number of species in stomach contents per individual was 2.75 ± 2.27 species (average ± SD; range: 1 to 7). The most frequently observed species was *L. argenteiventris* (%N = 35% and %FO = 50%), followed by *Decapterus* sp. (%N = 14% and %FO = 12.5%).

The records of body weight and wet weight of the stomach contents in one individual (#165: subadult male, 13 y old, found dead at the bottom of the water at about 0500 h) were 229.5 and 5.8 kg, respectively. The wet weight of the stomach contents was 2.54% of the body weight of this individual.

Cephalopod remains regurgitated by a dolphin were identified as *Ommastrephes bartramii* (16S rRNA, 99.6% identical; Cytb, 99% identical).

Discussion

Scarcity of Feeding During the Daytime

In this study, very few foraging behaviours were observed (underwater video data recorded foraging behaviour only 11 times during 318 surveys, and 74% of the dolphin-watching guides observed only one to 10 instances of foraging in one season). In addition, *T. aduncus* did not feed on several fishes continuously or did not feed in groups. The considered daily feed requirement of mature Indo-Pacific bottlenose dolphins is about 4 to 5% of their body weight in captivity (Wang, 2018). Thus, a mature 200 kg individual eats 8 to 10 kg a day, which is equal to 40 to 50 flying fishes (Exocoetidae) weighing 200 g. In the observation results, the maximum number of prey foraged by dolphins was just one. Meanwhile, an entangled individual (#165MS; 229.5 kg in weight) fed on 5.8 kg of prey, equalling 2.54% of its body weight. Although the food requirement of mature individuals in previous studies was slightly below this, it is possible that dolphins performed some concentrated foraging before entanglement from about 0400 to 0800 h. In addition, Morisaka et al. (2015) confirmed possible food-related sounds (e.g., rapid pulse repetitions following increasing echolocation clicks) during the night near Mikura Island and in shallow water by the stationed acoustic buoy.

From the above results, we considered that the diurnal foraging behaviour observed within the dolphin-watching area was not the primary foraging location. Dolphins may perform concentrated feeding outside of the observation time or study area.

Prey Species and Suggested Feeding Time and Location

In the present study, we confirmed 11 species of fish, seven species of cephalopod, and one species of crustacean as prey species, as well as 10 species of fish and one species of crustacean as potential prey species. This suggests that Indo-Pacific bottlenose dolphins in Mikura Island target various and regional species as prey. In this study, the habitats and environments were different compared to the other locations of previous studies; however, this result is consistent with previous reports that *T. aduncus* foraged on various and regional species (Amir et al., 2005; Yamazaki et al., 2008; Kiszka et al., 2014; Ansmann et al., 2015).

The distribution and migration of the identified prey species could broadly be divided into three patterns: (1) mesopelagic, (2) neritic, and (3) epipelagic (Table 4). Only neritic (*L. argenteiventris*) and epipelagic (Exocoetidae) species matched between the stomach contents and observation results. Mesopelagic species were not confirmed from observation results (Table 4). The mismatch of prey species between stomach contents and direct behavioural observations may result from variations in prey species with feeding time. Direct feeding observations were conducted at the sea surface of shallow coastal areas during daytime, resulting in many neritic and epipelagic species. Conversely, stomach contents may reflect feeding outside our observation times. All entangled individuals with undigested stomach contents were found between 0400 to 0800 h. In a captive *T. aduncus*, the muscles of *Cypselurus poecilopterus* and *Scomber japonicus* were digested in about 90 min (Ohizumi et al., 2019). Therefore, the stomach contents in this study may reflect prey species taken by the entangled dolphins from night time to early morning (0300 to 0700 h).

Based on the sparse nature of daytime foraging and the amount of stomach contents, it is possible that dolphins around Mikura Island feed at night rather than during the day. The reason for daytime foraging, although rare, will be discussed in the next section on foraging probability in both sexes.

Whether dolphins actively forage at night offshore, nearshore, or both remains unclear. Three entangled individuals had neritic species in their stomach contents (#259MS, #356FA, and #406MA; Table 3), and the other entangled individuals had species from several habitats at the same time. Therefore, these dolphins likely migrate offshore for mesopelagic species, such as squid, that generally perform diel vertical migration (Kobayashi & Yamaguchi, 1988; Sakurai, 2014) or nearshore. Since Mikura Island is a seamount (Figure 1), mesopelagic species are likely distributed near the coastal area around the island at night (Moulins & Würtz, 2005; Johnston et al., 2008). Passive acoustic monitoring may be effective for analysing the night-time foraging areas in more detail (Todd et al., 2009; Elliott et al., 2011).

Daytime Foraging Individuals

Foraging females were recorded in the daytime significantly more frequently than males, although daytime foraging was rare overall (Figure 2). Such a female bias is consistent with previous studies of foraging behaviour in other areas, which reported that females tended to perform more daytime foraging behaviour than males in Sarasota Bay, Florida, in the United States (*T. truncatus*) and Bunbury, Western Australia, in Australia (*T. aduncus*) (Barros & Wells, 1998; Sprogis et al., 2016, 2017).

There are two hypotheses from the physiological and social aspects for explaining the female bias in feeding habits. One physiological hypothesis is the difference in food requirements in regards to

Table 4. Prey species and their habitats according to each method. "Prey species" are shown in **bold**, and "potential prey species" are shown in roman font.

Habitat	Stomach contents	Observation results		
		Video analysis	Data from the public	Interviews
Mesopelagic (Kobayashi & Yamaguchi, 1988; Yamashita & Tanitsu, 2004; Sakurai, 2014)	***Beryx splendens***			
	Decapodiformes			
	Enoploteuthis chunii			
	Eucleoteuthis luminosa			
	Cranchiidae			
	Nealotus tripes			
	Ommastrephes bartramii			
	Onychoteuthis borealijaponica			
	Todarodes pacificus			
Neritic (Uchida, 1933; Hatooka, 1997; Kakuda et al., 2002, Watari, 2006; Soyano et al., 2015; Shishido, 2016)	***Albunea symnista***	***L. argenteiventris***	***Octopus* sp.**	*Calotomus* sp.
	***Decapterus* sp.**	*Prionurus scalprum*	***P. scalprum***	Decapoda
	Labracoglossa argenteiventris		Muraenidae	*Hyperoglyphe* sp.
	***Pempheris* sp.**		*Myrichthys maculosus*	Labridae
	Serranidae		*Parajulis poecilepterus*	*Spratelloides* sp.
Epipelagic (Tsukahara et al., 1957; Hirai, 1999; Okabe et al., 2009)	***Cypselurus agoo***	Exocoetidae	**Exocoetidae**	*Hyporhamphus* sp.
	Parexocoetus mento		Belonidae	*Katsuwonus* sp.
	Scomber australasicus			
	***Scomber* sp.**			

reproductive status: females need more food than males when they are pregnant or nursing (Kastelein et al., 2003). In addition, Miketa et al. (2018) reported that females with a calf spent less time diving to forage and increased their surface time to protect the calf from predators. Therefore, females not getting enough food at night could compensate for this by foraging during the daytime. The other hypothesis is the social learning hypothesis: female calves learn foraging techniques from their mothers or through matrilineal inheritance (Krützen et al., 2005; Bender et al., 2009). Therefore, females may tend to forage in the daytime to show their foraging technique to their calves.

In this study, we tested neither the association between diurnal foraging individuals and their reproductive status nor the difference between foraging behaviours of dolphins with and without calves due to the rarity of daytime foraging behaviour. Additional long-term data and precise analysis would be required to comment on these topics. Nonetheless, the findings of this study will contribute to revealing the physiological and social aspects of dolphin behaviour in the future.

Acknowledgments

We would like to thank the dolphin-watching tour captains and guides, members of identification research (MIDO), and public for providing information on foraging behaviours. Logistical support was provided by the Mikurashima Tourist Information Centre. We also thank the people of Mikura Island for their kind support during our stay on the island. We would like to thank Editage (www.editage.com) for English language editing. This research was partially supported by the Cooperation Research Program of the Wildlife Research Center, Kyoto University, for R. Takahashi, JSPS KAKENHI Grant Number 15H05709 for T. Morisaka, and Grant Numbers 16K17367 and 20K12584 for M. Sakai.

Literature Cited

Amir, O. A., Berggren, P., Ndaro, S. G., & Jiddawi, N. S. (2005). Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. *Estuarine, Coastal and Shelf Science*, *63*(3), 429-437. https://doi.org/10.1016/j.ecss.2004.12.006

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*(3), 403-410. https://doi.org/10.1016/S0022-2836(05)80360-2

Ansmann, I. C., Lanyon, J. M., Seddon, J. M., & Parra, G. J. (2015). Habitat and resource partitioning among Indo-Pacific bottlenose dolphins in Moreton Bay, Australia. *Marine Mammal Science*, *31*(1), 211-230. https://doi.org/10.1111/mms.12153

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, *79*(3), 1045-1059. https://doi.org/10.2307/1383114

Bender, C. E., Herzing, D. L., & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition*, *12*(1), 43-53. https://doi.org/10.1007/s10071-008-0169-9

Bouveroux, T. N., Caputo, M., Froneman, P. W., & Plön, S. (2018). Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: Trends and potential drivers. *Marine Mammal Science*, *34*(3), 645-665. https://doi.org/10.1111/mms.12471

Chin, T. C., Adibah, A. B., Hariz, Z. D., & Azizah, M. S. (2016). Detection of mislabelled seafood products in Malaysia by DNA barcoding: Improving transparency in food market. *Food Control*, *64*, 247-256. https://doi.org/10.1016/j.foodcont.2015.11.042

Clarke, M. R. (Ed.). (1986). *A handbook for the identification of cephalopod beaks*. Clarendon Press.

Connor, R. C., Sakai, M., Morisaka, T., & Allen, S. J. (2019). The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 345-368). Springer.

Dudzinski, K. M., Gregg, J. D., Paulos, R. D., & Kuczaj II, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. *Behavioural Processes*, *84*(2), 559-567. https://doi.org/10.1016/j.beproc.2010.02.013

Elliott, R. G., Dawson, S. M., & Henderson, S. (2011). Acoustic monitoring of habitat use by bottlenose dolphins in Doubtful Sound, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *45*(4), 637-649. https://doi.org/10.1080/00288330.2011.570351

Hanson, M. T., & Defran, R. H. (1993). The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquatic Mammals*, *19*(3), 127-142.

Hatooka, K. (1997). Pempheridae. In O. Okamura & K. Amaoka (Eds.), *Japanese saltwater fish* (pp. 380-381). Yama-kei Publishers.

Hirai, K. (1999). 伊豆諸島海域におけるゴマサバの漁場形成と水温 [Water temperature and fishing grounds for spotted mackerels around the Izu Islands]. *Japanese Society of Fisheries Oceanography*, *63*(4), 199-204.

Irvine, A. B., Scott, M. D., Wells, R. S., & Kaufmann, J. H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*(4), 671-688.

Jansen, O. E., Michel, L., Lepoint, G., Das, K., Couperus, A. S., & Reijnders, P. J. (2013). Diet of harbor porpoises along the Dutch coast: A combined stable isotope and stomach contents approach. *Marine Mammal Science*, *29*(3), E295-E311. https://doi.org/10.1111/j.1748-7692.2012.00621.x

Johnston, D. W., McDonald, M., Polovina, J., Domokos, R., Wiggins, S., & Hildebrand, J. (2008). Temporal patterns in the acoustic signals of beaked whales at Cross Seamount. *Biology Letters*, *4*(2), 208-211. https://doi.org/10.1098/rsbl.2007.0614

Kakuda, T., Tajima, Y., Arai, K., Kogi, K., Hishii, T., & Yamada, T. K. (2002). On the resident "bottlenose dolphins" from Mikura water. *Memoirs of the National Science Museum (Tokyo)*, *38*, 255-272.

Kastelein, R. A., Staal, C., & Wiepkema, P. R. (2003). Food consumption, food passage time, and body measurements of captive Atlantic bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *29*(1), 53-66. https://doi.org/10.1578/016754203101024077

Kiszka, J. J., Méndez-Fernandez, P., Heithaus, M. R., & Ridoux, V. (2014). The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. *Marine Biology*, *161*(4), 953-961. https://doi.org/10.1007/s00227-014-2395-9

Kita, Y., Kawase, M., Kogi, K., & Murayama, M. (2018). 御蔵島ミナミハンドウイルカ (*Tursiops aduncus*) における食性解析 [Analysis of feeding habitat in Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) on Mikura Island, Japan]. *DNA Polymorphism*, *26*(1), 51-55.

Kobayashi, H., & Yamaguchi, Y. (1988). Studies on fishing depth and difference in catch by color of jigs for purple-back flying squid *Symplectoteuthis oualaniensis* and luminous flying squid *Eucleoteuthis luminosa*. *Japanese Society of Fisheries Science*, *54*(6), 919-927. https://doi.org/10.2331/suisan.54.919

Kogi, K., Hishii, T., Imamura, A., Iwatani, T., & Dudzinski, K. M. (2004). Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science*, *20*(3), 510-526. https://doi.org/10.1111/j.1748-7692.2004.tb01176.x

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(25), 8939-8943. https://doi.org/10.1073/pnas.0500232102

Kubodera, T. (2005). *Manual for the identification of cephalopod beaks in the northwest Pacific* (Version 1-1). https://www.kahaku.go.jp/research/db/zoology/Beak-E/index.htm

Miketa, M. L., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., & Mann, J. (2018). Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. *Animal Behaviour*, *137*, 107-117. https://doi.org/10.1016/j.anbehav.2017.12.023

Mizrahi, N., Kerem, D., Goffman, O., Lernau, O., & Spanier, E. (2009). Identified fish remains regurgitated by a solitary Indian Ocean bottlenose dolphin, *Tursiops aduncus*, in the Gulf of Aqaba (Mammalia: Delphinidae). *Zoology in the Middle East*, *46*(1), 19-28. https://doi.org/10.1080/09397140.2009.10638323

Morisaka, T., Sakai, M., & Kogi, K. (2015). Detection of the nighttime distribution of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island with stationed acoustic buoys. *Bulletin of Institute of Oceanic Research and Development, Tokai University*, *36*, 1-7. https://doi.org/10.1578/AM.43.6.2017.585

Moulins, A., & Würtz, M. (2005). Occurrence of a herd of female sperm whales and their calves (*Physeter catodon*), off Monaco, in the Ligurian Sea. *Journal of the Marine Biological Association of the United Kingdom*, *85*(1), 213-214. https://doi.org/10.1017/S0025315405011094h

Nakabou, T. (2000). 日本産魚類検索 全種の同定(第二版) [Fishes of Japan with pictorial keys to the species (2nd ed.)]. Tokai University Press.

Nakasuji, A. (2012). 御蔵島海域におけるミナミハンドウイルカ (*Tursiops aduncus*) の日中の環境利用 [Daytime habitat use of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island] (Master's thesis). Kyoto University, Kyoto, Japan. https://www.wrc.kyoto-u.ac.jp/ResearchThemes.html

Ohe, F. (1985). *Marine fish-otoliths of Japan*. Senior High School Attached to the Aichi University of Education.

Ohizumi, H., Koide, M., Kusakabe, H., Ueda, K., Yanagisawa, M., & Koga, H. (2019). Digestion process of ingestion in forestomach of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). *Journal of the School of Marine Science and Technology*, *Tokai University*, *17*, 1-9.

Ohtsuka, S., Shimono, T., Hanyuda, T., Shang, X., Huang, C., Soh, H. Y., Kimmerer, W., Kawai, H., Itoh, H., Ishimaru, T., & Tomikawa, K. (2018). Possible origins of planktonic copepods, *Pseudodiaptomus marinus* (Crustacea: Copepoda: Calanoida), introduced from East Asia to the San Francisco Estuary based on a molecular analysis. *Aquatic Invasions*, *13*(2), 221-230. https://doi.org/10.3391/ai.2018.13.2.04

Okabe, K., Iwata, S., & Watanabe, S. (2009). Implication of effects of fluctuations in oceanographic condition and maturation process on migration of common mackerel (*Scomber japonicus*) in the fishing grounds around Izu [Japan] Islands. *Bulletin of the Japanese Society of Fisheries Oceanography*, *Japan*, *73*(1), 1-7.

Rivaton, J., & Bourret, P. (Eds.). (1999). *Les otolithes des poissons de l'Indo-Pacifique* [Otoliths of the Indo-Pacific fishes]. Institut de Recherche pour le Développement.

Sakai, M., Morisaka, T., Kogi, K., Hishii, T., & Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes*, *83*(1), 48-53. https://doi.org/10.1016/j.beproc.2009.10.001

Sakai, M., Kita, Y. F., Kogi, K., Shinohara, M., Morisaka, T., Shiina, T., & Inoue-Murayama, M. (2016). A wild Indo-Pacific bottlenose dolphin adopts a socially and genetically distant neonate. *Scientific Reports*, *6*, 23902. https://doi.org/10.1038/srep23902

Sakurai, Y. (2014). スルメイカの繁殖生態と気候変化に応答する資源変動 [Resource change in response to breeding ecology and climate change of *Todarodes pacificus*]. *Fisheries Promotion*, *48*(7), 1-54. www.suisan-shinkou.or.jp/promotion/pdf/SuisanShinkou_559.pdf

Samarra, F. I. P., Bassoi, M., Béesau, J., Elíasdóttir, M. Ó., Gunnarsson, K., Mrusczok, M. T., Rasmussen, M., Rempel, J. N., Thorvaldsson, B., & Víkingsson, G. A. (2018). Prey of killer whales (*Orcinus orca*) in Iceland. *PLOS ONE*, *13*(12), e0207287. https://doi.org/10.1371/journal.pone.0207287

Shishido, H. (2016). 資料海外のサイトで紹介されているスジアラの資源生態等に関する総説の紹介 [Introduction of the review about resource ecology etc. of *Plectropomus leopardus* introduced on the site of overseas site]. *Kagoshima Industrial Technology Center Research Report*, *6*, 21-27.

Smith, H. C., & Sprogis, K. R. (2016). Seasonal feeding on giant cuttlefish (*Sepia apama*) by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in south-western Australia. *Australian Journal of Zoology*, *64*(1), 8-13. https://doi.org/10.1071/ZO150755

Soyano, K., Teruya, K., & Tyuta, H. (Eds.). (2015). ハタ科魚類の水産研究最前線 [Frontiers of fisheries science in groupers]. Kouseisha Kouseikaku.

Sprogis, K. R., Raudino, H. C., Hocking, D., & Bejder, L. (2017). Complex prey handling of octopus by bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, *33*(3), 934-945. https://doi.org/10.1111/mms.12405

Sprogis, K. R., Pollock, K. H., Raudino, H. C., Allen, S. J., Kopps, A. M., Manlik, O., Tyne, J. A., & Bejder, L. (2016). Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Frontiers in Marine Science*, *3*, 12. https://doi.org/10.3389/fmars.2016.00012

Todd, V. L., Pearse, W. D., Tregenza, N. C., Lepper, P. A., & Todd, I. B. (2009). Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES Journal of Marine Science*, *66*(4), 734-745. https://doi.org/10.1093/icesjms/fsp035

Trites, A. W., & Spitz, J. (2018). Diet. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 255-259). Academic Press.

Tsukahara, H., Shiokawa, T., & Inao, T. (1957). Studies on the flying-fishes of the Amakusa Islands: Part 3. The life histories and habits of three species of the genus *Cypselurus* (1). *Science Bulletin of the Faculty of Agriculture, Kyushu University*, *16*(2), 287-302.

Uchida, K. (1933). ハタンポの生活史及び他のハタンポ科の魚数種の幼期に就いて [Life history of *Pempheris japonicus*, and juveniles of other species in genus *Pempheris*]. *Zoological Science*, *45*(535), 207-218.

Vaughn, R., Würsig, B., & Packard, J. (2010). Dolphin prey herding: Prey ball mobility relative to dolphin group and prey ball sizes, multispecies associates, and feeding duration. *Marine Mammal Science*, *26*(1), 213-225. https://doi.org/10.1111/j.1748-7692.2009.00317.x

Wang, J. Y. (2018). Bottlenose dolphin, *Tursiops aduncus*, Indo-Pacific bottlenose dolphin. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 125-130). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00073-X

Watari, S. (2006). A study on the population dynamics of yellowstriped butterfish in the waters around the northern part of the Izu Islands. *Bulletin of Fisheries Research Agency*, *18*, 167-242.

Wen, J., Tinacci, L., Acutis, P. L., Riina, M. V., Xu, Y., Zeng, L., Ying, X., Chen, Z., Guardone, L., Chen, D., Sun, Y., Zhao, J., Guidi, A., & Armani, A. (2017). An insight into the Chinese traditional seafood market: Species characterization of cephalopod products by DNA barcoding and phylogenetic analysis using *COI* and *16SrRNA* genes. *Food Control*, *82*, 333-342. https://doi.org/10.1016/j.foodcont.2017.07.011

Yamashita, N., & Tanitsu, A. (2004). 春季の黒潮親潮移行域および黒潮続流域におけるフウライカマス *Nealotus tripes* の分布と食性 [Distribution and feeding habits of black snake mackerel *Nealotus tripes* in the Kuroshio extension in spring]. *Bulletin of the Japanese Society of Fisheries Oceanography*, *68*(4), 239-244.

Yamazaki, T., Oda, S. I., & Shirakihara, M. (2008). Stomach contents of an Indo-Pacific bottlenose dolphin stranded in Amakusa, western Kyushu, Japan. *Fisheries Science*, *74*(5), 1195-1197. https://doi.org/10.1111/j.1444-2906.2008.01640.x