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Stomach contents of small cetaceans stranded along the Sea of Oman and Arabian Sea coasts of the Sultanate of Oman

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*This study examined the stomach contents of 11 bottlenose dolphins (*Tursiops sp.*), five Indo-Pacific humpback dolphins (*Sousa chinensis*) and two spinner dolphins (*Stenella longirostris*) that were found stranded along the Omani coastline. Across the three species examined, a total of 4796 fish otoliths and 214 cephalopod beaks were found, representing at least 33 species in 22 families. Prey item importance was calculated using the percentage by number and percentage by frequency of occurrence methods, and a modified index of relative importance. The fish families Apogonidae, Carangidae and Scombridae were the most numerically important prey of the bottlenose dolphins. Sciaenidae was the most numerically important fish family for the Indo-Pacific humpback dolphins. The myctophid *Benthosema pterotum* formed the majority of the prey items of spinner dolphins. Cephalopod remains found in the stomach samples were represented by the families Sepiidae, Loliginidae and Onychoteuthidae. The known depth distribution of prey items of bottlenose dolphins indicated that the animals fed in a wide variety of habitats. Indo-Pacific humpback dolphin prey items indicated feeding in shallow coastal areas. Spinner dolphins appear to have exploited the upper 200 m of the water column for food, where their vertically migrating mesopelagic prey are found at night. Most prey species found in the stomach contents do not appear to be of current commercial importance in Oman. However, the findings here indicated that all three species of dolphins were feeding in areas where artisanal and/or commercial fishing occurs and has conservation implications.*

Keywords: cetaceans, stomach contents, diets, feeding, habitat, Sea of Oman, Gulf of Masirah, Oman

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INTRODUCTION

Dietary analysis is an important aspect of research into the feeding ecology of animals. It enables the quantification of a species' nutritional needs (Benoit-Bird, 2004), and of the amount of food consumed by an individual or population (Hyslop, 1980). It also enables the estimation of predation pressure on the prey fauna (Robison & Craddock, 1983) and in the case of cetaceans, assists in the exploration of the hypothesis that distribution is closely linked to the distribution and abundance of prey (Hui, 1985; Selzer & Payne, 1988; Bowen & Siniff, 1999). Methods of studying the feeding ecology of cetaceans include stable-isotope and fatty acids composition analysis (Niño-Torres *et al.*, 2006), trace metal measurements (Lahaye *et al.*, 2005), fecal analysis (Smith & Whitehead, 2000) and the examination of stomach contents (Di Beneditto & Siciliano, 2007).

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Overall, relatively little study has been conducted on the diets of cetaceans in the northern Indian Ocean. Baldwin (2003) briefly mentioned the stomach contents of bottlenose dolphins (*Tursiops truncatus*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) found on Merawah and Bu Tina Islands in Abu Dhabi. Robineau & Fiquet (1994) examined the stomach contents of a single juvenile male bottlenose dolphin found along the Arabian Gulf coast of Saudi Arabia. There is also some published information on the diets of marine cetaceans in India, comprising studies on the stomach contents of eight cetacean species collectively, including the three species examined here (Natarajan & Rajaguru, 1983, 1985; Karbhari *et al.*, 1985; Silas *et al.*, 1985; Krishnapillai & Kasinathan, 1987; Krishnan *et al.*, 2007). A thorough search of the literature on marine cetacean dietary studies revealed no results for Pakistan, Iran and Sri Lanka.

To date, knowledge about the diets of cetaceans in the Sultanate of Oman is very limited, though there have been basic observations of feeding behaviour (Salm, 1991; Baldwin *et al.*, 1998, 2004). This study analyses the stomach contents of stranded, beach-cast bottlenose dolphins

(*Tursiops* sp.), Indo-Pacific humpback dolphins (*Sousa chinensis*) and spinner dolphins (*Stenella longirostris*) with the aims of better understanding the distribution and patterns of habitat use of these dolphin species in Oman, of assessing whether the dolphins could be competing with local fisheries for resources, and of considering whether there is evidence of niche partitioning between dolphin species with overlapping distributions.

MATERIALS AND METHODS

Sample collection sites

Stomach contents samples were collected from cetaceans found during dedicated and opportunistic beach surveys along the Oman coastline, and opportunistically during any stranding events that were reported. Dedicated surveys were conducted from 2000 to 2003, covering 534 km of beaches from Muscat in the north, to Dhofar, and from 2005 to 2006, covering over 565 km of beaches from As Sahm on the Al Batinah coast, south to the island of Masirah. These surveys yielded a total of 18 individual carcasses representing three species; the bottlenose dolphin, Indo-Pacific humpback dolphin and spinner dolphin and provided the samples examined in this study (Figure 1). The carcasses were found in varying states of decomposition and were therefore categorized according to 'stranding states', using definitions provided by Geraci & Lounsbury (2005) (Table 1).

COLLECTION OF STOMACH CONTENTS SAMPLES

Stranded beach-cast cetaceans were dissected *in situ* upon discovery, to locate any food remains in the stomach and oesophagus following established methods for stomach contents collection (e.g. Sekiguchi, 1995; Dolar *et al.*, 2003). The stomach and oesophagus were first removed from the body cavity. To ensure that prey items were not lost upon removal, the stomach and oesophagus were turned inside out, placed over a series of simple kitchen sieves with a maximum mesh size of 2 mm and rinsed thoroughly using a hose. If available, otoliths were extracted directly from the intact skulls of fish in the sample while length measurements of whole or semi-digested prey that was still relatively intact were taken. Stomach contents with whole or semi-digested prey were left soaking in water for a few days, and then rinsed to separate the soft tissues of the prey items from the bony parts. The samples were then sieved multiple times over a collecting tray using sieves of decreasing mesh size, reducing the stomach contents to cephalopod beaks, fish otoliths, fish scales and bones. The otoliths, fish scales and bones were then left to dry, while cephalopod beaks were stored in 70% ethanol. Eight of the stomachs were full, seven were less than half-full, and no information on stomach fullness was available for the remaining two stomach samples that were collected by associate researchers (Table 1).

Identification and enumeration of prey items

Each dried stomach contents sample was sorted into fish otoliths, fish dentary bones, other fish bones and scales, and cephalopod beaks. The otoliths and dentary bones were sorted into left and right, while the beaks were sorted into upper and lower, and these were itemized. Otoliths were further sorted according to type (i.e. shape, size and pattern), and matched into pairs when both left and right sides of equal sizes were available (i.e. one right and left otolith that matched in pattern and size equated to one otolith pair). The number of fish eaten was estimated by counting the number of otolith pairs plus any other unpaired otoliths (i.e. each otolith pair was considered to be one fish, while remaining unpaired otoliths that were different from each other in pattern and size were counted as one fish each). Due to their very small size and high abundance, the otoliths in each spinner dolphin sample were tallied and divided by two to estimate the total number of fish consumed (Dolar *et al.*, 2003). The higher count of either upper or lower cephalopod beaks in each sample was used to estimate the number of cephalopods consumed (Pinkas *et al.*, 1971; Dolar *et al.*, 2003; Amir *et al.*, 2005). Fish dentary bones were used to estimate the number of fish consumed when a sample did not contain any otoliths. In samples where both otoliths and fish dentary bones were available, the dentary bones were identified and included in the analysis only if they did not match with any species that had already been identified by otoliths.

Otoliths were identified to the lowest taxonomic level possible using Smale *et al.* (1995) while cephalopod beaks were identified to the lowest taxonomic level possible using Clarke (1986) and Kubodera (2005). Reference collections specific to Oman and the Middle East are not available. The identification of fish dentary bones was made by K. Longenecker (Bishop Museum, Honolulu, Hawaii, USA). Cephalopod beaks that could not be identified were sent to M. Begoña Santos (Centro Oceanográfico de Vigo, Spain) and S. Plön (South African Institute for Aquatic Biodiversity), but remained unidentified due to the absence of matching samples from their respective work regions. Fish classification and information on fish distribution and habitat followed Al-Abdessalam (1995) and Randall (1995) while similar information for cephalopods followed Al-Abdessalam (1995) and Jereb & Roper (2005). An attempt was made to use fish otolith lengths, and rostral and hood lengths of cephalopod beaks to back-calculate the masses and standard lengths of the fish and cephalopods that were consumed. However, due to the lack of available regression equations and allometric coefficients for most of the fish species and various cephalopod species in Oman, these measurements were not utilized in this study.

Calculation of prey importance

Following the equations used in Sekiguchi (1995) and Amir *et al.* (2005), three different indices were used to quantify the occurrence and relative importance of prey items in the stomachs: (1) percentage by number (%N); (2) percentage frequency of occurrence (%FO); and (3) the modified index of relative importance (IRI).

Percentage by number (%N) is the calculation of the numerical abundance ($\%N_i$) of each prey species present in the diet. This was calculated as:

$$\%N = (N_{ij}/N_j)^{*}100$$

where N_{ij} is the number of prey species i present in stomach j, and N_j is the total number of prey present in stomach j.

Percentage frequency of occurrence (%FO) is the calculation of the frequency of occurrence of each prey species

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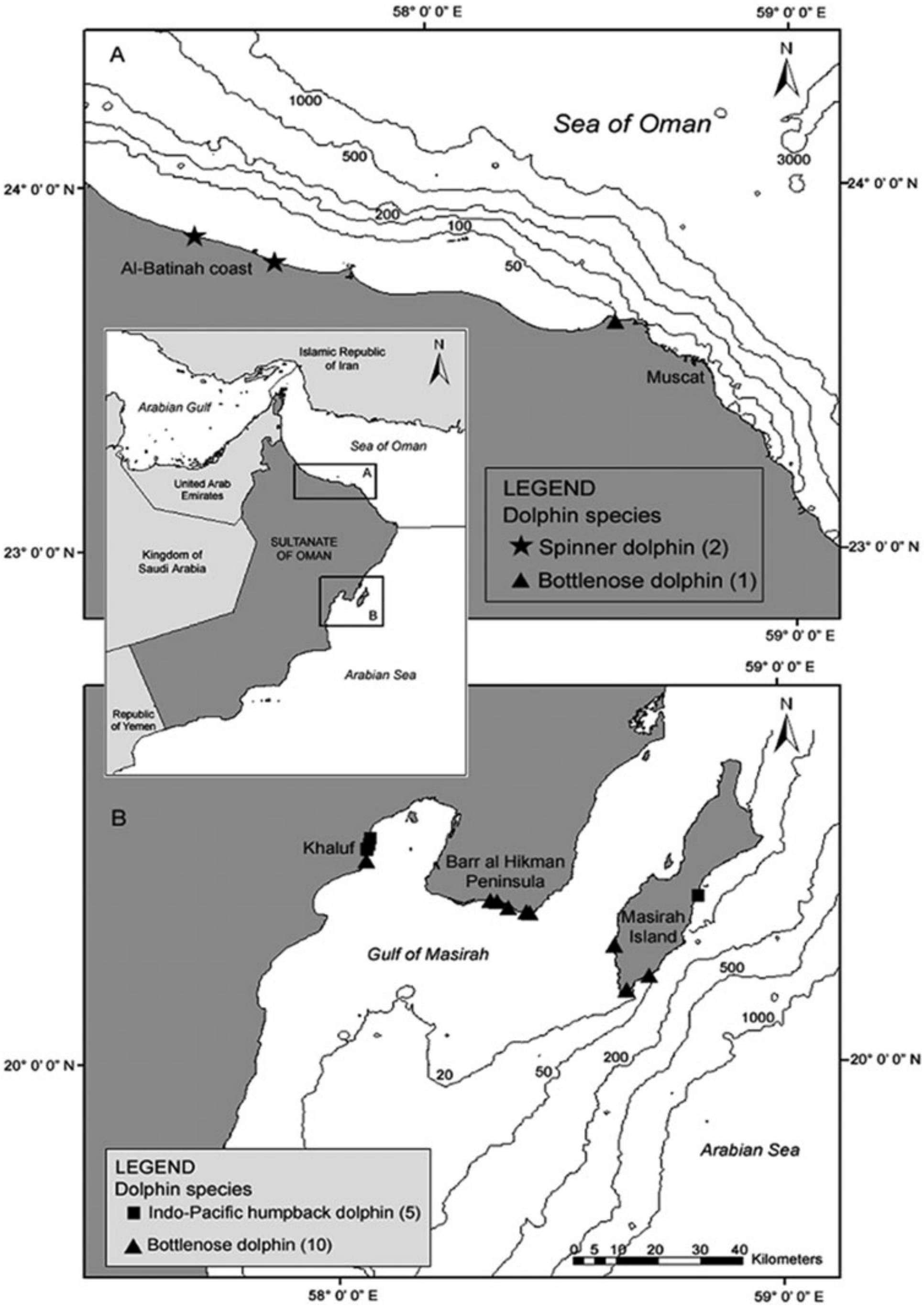

Fig. 1. Maps showing (inset) the location of Oman, and the locations at which stomach contents of stranded bottlenose, Indo-Pacific humpback and spinner dolphins were collected during dedicated and incidental beach surveys in (A) Muscat/Sea of Oman and (B) Gulf of Masirah regions. Numbers in parentheses in the legends indicate the sample size for each dolphin species. Depth contours are in metres.

($\%FO_i$) within the stomach samples. This was calculated as:

$$\%FO = (FO_{ij}/F_j)^{*}100$$

where FO_{ij} is the frequency of stomachs i containing prey j, and F_j is the total number of stomachs containing prey remains.

The index of relative importance is a rank measure of the importance of different prey species in the diet. This was calculated as a modified version of Pinkas *et al.* (1971) (in Sekiguchi (1995)):

$$IRI = \%N^{*}\%FO$$

Percentage similarity (PS) was calculated to investigate dietary overlap between stomachs of the same species, as well as interspecific dietary overlap, using the equation in Silver (1975). This was calculated as:

$$PS_{ab} = \Sigma \min(\%N_{ia}, \%N_{ib})$$

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Table 1. Summary of stomach samples analysed. Stranding state (SS) definition (i.e. code for condition of animal/carcass) is based on Geraci & Lounsbury (2005). SS: 1 = live animal; 5 = skeletal remains. Stomach fullness (SF): 8/8 = full.

Sample number	Species	Sex	Body length (cm)	Location	SS (1–5)	SF (8/8)
26-05-01-03	*Tursiops* sp.	U	196	Barr al Hikman	5	N/A
29-09-01-05	*Tursiops* sp.	U	N/A	Barr al Hikman	4	8
29-09-01-06	*Tursiops* sp.	M	260	Barr al Hikman	4	8
04-10-01-01	*Tursiops* sp.	M	253	Masirah Island	3	1
09-10-01-01	*Tursiops* sp.	U	246	Masirah Island	5	N/A
22-10-01-09	*Tursiops* sp.	U	216	Masirah Island	4	8
01-11-01-01 BaH	*Tursiops* sp.	U	N/A	Barr al Hikman	5	8
01-11-01-03 BaH	*Tursiops* sp.	M	220	Barr al Hikman	5	8
05-11-01-01	*Tursiops* sp.	M	210	Khaluf	5	8
15-02-06-01	*Tursiops* sp.	M	226	Masirah Island	3	8
02-05-06-01	*Tursiops* sp.	U	275	Muscat	3	8
16-12-01-01A	*Sousa chinensis*	F	268	Khaluf	2	3
16-12-01-05A	*Sousa chinensis*	F	257	Khaluf	3	3
29-12-01-05	*Sousa chinensis*	M	250	Khaluf	3	1
29-12-01-06	*Sousa chinensis*	F	245	Khaluf	4	2
24-02-06-02	*Sousa chinensis*	U	226	Masirah Island	5	<1
27-08-05-01	*Stenella longirostris*	M	171	Al Batinah	4	8
27-08-05-02	*Stenella longirostris*	M	130*	Al Batinah	3	3

*, length measured to caudal peduncle, as tail flukes had been severed; U, unidentified; M, male; F, female.

where a and b represent different stomachs and i represents the prey species.

RESULTS

A total of 4796 fish otoliths and 214 cephalopod beaks (upper and lower) were found in the 18 stomachs (across all three species) of cetaceans examined. No crustacean or other remains were found. Eleven stomachs of bottlenose dolphins were examined, of which 18.0% (2) contained only fish remains, 27.0% (3) contained only cephalopod remains, and 55.0% (6) contained both fish and cephalopod remains. In terms of number, 71.0% of the diet of bottlenose dolphins comprised fish, while the remainder 29.0% comprised cephalopods. A total of five stomachs of Indo-Pacific humpback dolphins were examined, of which 20.0% (1) contained both fish and cephalopod remains, while 80.0% (4) of stomachs contained only fish remains. In terms of number, 87.0% of the diet of humpback dolphins comprised fish, while the remaining 13.0% comprised cephalopods. Two stomachs of spinner dolphins were examined, and both fish and cephalopod remains were found in each. Combining data from the two specimens, 99.0% of the total number of prey remains found in the spinner dolphin stomachs comprised fish, while the remaining 1.0% comprised cephalopods. There was not any prey species overlap between bottlenose dolphins and spinner dolphins or between Indo-Pacific humpback dolphins and spinner dolphins. Only one prey species overlapped between bottlenose dolphins and Indo-Pacific humpback dolphins (i.e. *Otolithes ruber*) and one genus overlapped between bottlenose dolphins and spinner dolphins (i.e. *Apogon*). However, the total percentage number of *Apogon* fish found in the stomachs of bottlenose dolphins was much higher than in spinner dolphins (56.1% versus 0.05%).

Bottlenose dolphins

A total of 416 whole sagittal otoliths from an estimated 228 individual fish were found in the stomachs of eight of the 11 bottlenose dolphins sampled (Table 2). These represented 22 species of teleost fish distributed across 20 genera and 14 families. Numerically, the most important prey family was the Apogonidae (cardinalfish), in which two of three species present, *Apogon cyanosoma* and *A. multitaeniatus*, accounted for 55.2% of all fish prey consumed (Table 2). Apogonidae, Scombridae and Sciaenidae were the most frequently occurring families (36.4% each) (Table 2). Of the otoliths found in the bottlenose dolphins' stomachs, 1.4% were broken or degraded severely, preventing identification and were thus not included in analysis.

In terms of relative importance, the family Apogonidae had the highest modified IRI (2042.0) (Table 2). *Apogon multitaeniatus* ranked first in terms of number (32.0%) and had the highest modified IRI (582.4), although *Otolithes ruber*, *Scomber japonicus* and *Terapon jarbua* occurred more frequently (27.3% each). *Apogon cyanosoma* ranked second in terms of number and modified IRI (23.2%, 422.2), but also did not occur as frequently as the former three species. *Carangoides malabaricus* ranked third in terms of number (11.8%), but only occurred in one stomach (%FO = 9.1), whereas *O. ruber*, *S. japonicus* and *T. jarbua* each made up only approximately 6.0% in terms of number, though the three ranked first in frequency of occurrence. *Otolithes ruber* also had a higher modified IRI than *C. malabaricus* (166.5 versus 107.4). One prey species (*Epinephelus* sp.) only accounted for <5.0% in terms of number while all other prey species found in the stomachs accounted for <1.0% each in terms of number (Table 2). The average number of fish prey taxa per stomach was 3.6 (± SD 1.6). The number of fish prey items found per stomach ranged from 0–127 (mean = 21.1, ± SD 37.2, N = 11). Percentage similarity (PS) calculations across dolphin samples revealed low levels of overlap in fish prey species found in the diet. Only one pair of stomachs, both from individuals from the Gulf of Masirah, had PS >50.0%, while 19 of the 28 stomach pairs (67.9%) had a PS of 0.0. The stomach contents of the single dolphin from Muscat (Sea of Oman) had a PS of 0.0 compared with all the other stomach contents of the Gulf of Masirah dolphins (Table 3) and its mainly pelagic prey species are

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Table 2. Percentage number and percentage frequency of occurrence of fish and cephalopod families and species found in stomachs of bottlenose dolphins. IRI, index of relative importance; n_s, total number of stomachs containing prey items; *, prey items of sole bottlenose dolphin found in Muscat; **, lower beak count.

Prey species	N	% number	F	% frequency	Modified IRI
Fish					
Family Apogonidae	128	56.1	4	36.4	2042.0
Apogon cookii	2	0.9	2	18.2	16.4
Apogon cyanosoma	53	23.2	2	18.2	422.2
Apogon multitaeniatus	73	32.0	2	18.2	582.4
Family Carangidae	29	12.7	2	18.2	231.1
Carangoides malabaricus	27	11.8	1	9.1	107.4
Selar crumenophthalmus	2	0.9	1	9.1	8.2
Family Engraulidae	2	0.9	2	18.2	16.4
Thryssa setirostris	2	0.9	2	18.2	16.4
Family Gerreidae	1	0.4	1	9.1	3.6
Gerres oyena	1	0.4	1	9.1	3.6
Family Kyphosidae	1	0.4	1	9.1	3.6
Kyphosid 1	1	0.4	1	9.1	3.6
Family Mullidae	2	0.9	2	18.2	16.4
Parupeneus rubescens	1	0.4	1	9.1	3.6
*Upeneus tragula**	1	0.4	1	9.1	3.6
Family Nemipteridae	1	0.4	1	9.1	3.6
Scolopsis vosmeri	1	0.4	1	9.1	3.6
Family Sciaenidae	16	7.0	4	36.4	254.8
Otolithes ruber	14	6.1	3	27.3	166.5
Umbrina canariensis	2	0.9	2	18.2	16.4
Family Scombridae	19	8.3	4	36.4	302.1
*Gymnosarda unicolor**	1	0.4	1	9.1	3.6
Katsuwonus pelamis	3	1.3	1	9.1	11.8
Scomber japonicus	14	6.1	3	27.3	166.5
*Thunnus albacares**	1	0.4	1	9.1	3.6
Family Serranidae	9	3.9	1	9.1	35.5
Epinephelus sp.	9	3.9	1	9.1	35.5
Family Sparidae	2	0.9	1	9.1	8.2
Crenidens crenidens	2	0.9	1	9.1	8.2
Family Sphyraenidae	1	0.4	1	9.1	3.6
Sphyraena jello	1	0.4	1	9.1	3.64
Family Teraponidae	15	6.6	3	27.3	180.2
Terapon jarbua	15	6.6	3	27.3	180.2
Family Trichiuridae	2	0.9	2	18.2	16.4
Trichiurus lepturus	2	0.9	2	18.2	16.4
Fish totals	228	100.0			
Cephalopods					
Family Sepiidae	30	37.5	8	72.7	2727.3
Sepia pharaonis	23	28.8	7	63.6	1831.7
Sepia latimanus	5	6.3	2	18.2	114.7
Sepia sp.	2	2.5	2	18.2	45.5
Family Loliginidae	2	2.5	1	11.1	22.7
Loligo sp.	2	2.5	1	9.1	22.7
Unidentified sp. 1	2	2.5	1	9.1	27.8
Unidentified sp. 2	38	47.5	4	36.4	1727.3
Unidentified sp. 3	8	10.0	3	27.3	272.7
Cephalopod totals	80**	100.0			
Total	308	100.0	$n_s = 11$		

indicated in Table 2. A total of 174 cephalopod beaks from 95 cephalopods (squids and cuttlefish) were found in nine of the 11 bottlenose dolphin stomachs examined, all of which were from the Gulf of Masirah. These beaks represented at least four species in two genera and two families, namely the Sepiidae and Loliginidae (Table 2). There were three other unidentified species that accounted for 60.0% (48) of the lower beaks that were analysed.

INDO-PACIFIC HUMPBACK DOLPHINS

A total of 21 otoliths from 13 teleost fish were found in the stomachs of the five Indo-Pacific humpback dolphins sampled (Table 4). These represented five species in four genera and three families that occur predominantly in turbid, shallow water habitats. Numerically, the most important prey family was Sciaenidae (53.9%), followed by Ariidae (30.8%) and Synodontidae (15.4%). The most frequently occurring prey family was Sciaenidae (100.0%). *Arius* sp. was the most important prey species in terms of number (30.8%) though it only had a frequency of occurrence of 20.0%. The sciaenids *Johnius* sp. and *Otolithes ruber* each ranked second in terms of number (23.1%). However, *O. ruber* occurred more frequently than *Johnius* sp. (60.0% versus 40.0%) (Table 4). *Otolithes ruber* had the highest modified IRI (1384.8), followed by *Johnius* sp. (923.2) and *Arius* sp. (615.4) (Table 4). The average number of fish prey taxa per stomach was 1.4 ($\pm$ SD 0.9). The number of fish prey items found per stomach ranged from 1–7 (mean = 2.6, $\pm$ SD 2.6, N = 5). PS calculations across samples revealed minimal overlap in fish prey species found in the stomachs. Only one pair of stomachs had PS > 50.0%, while 6 of the 10 stomach pairs had a PS of 0.0 (Table 3). Only one of the five Indo-Pacific humpback dolphin stomachs that were examined contained cephalopod beaks. These comprised one upper and two lower beaks and represented two squids in total, but were not successfully identified due to a lack of comparable beaks from the region.

Spinner dolphins

A total of 4355 sagittal otoliths from 2179 fishes were found in the stomachs of the two spinner dolphins sampled (Table 5). These represented five species in at least four genera and four families of teleost fish that occurred almost entirely in mesopelagic water depths. The Myctophidae was the most important prey family in terms of number and frequency of occurrence (99.4% and 100.0% respectively). Due to the small sample size of two dolphins, the modified IRI for spinner dolphins was not calculated. A total of 23 upper beaks and 14 lower beaks were retrieved from both spinner dolphins that were sampled. These all represented *Onychoteuthis banksi* from the family Onychoteuthidae (Table 5).

DISCUSSION

Bottlenose dolphins

The results show that the bottlenose dolphins examined in this present study consumed a relatively large variety of prey (Table 2). However, it was evident that the diet of dolphins from the Gulf of Masirah and of the single animal from Muscat differed in terms of preferred habitat of prey species. The depth distributions of the majority of prey species of bottlenose dolphins from the Gulf of Masirah suggest that the dolphins there fed primarily in shallow, coastal inshore waters and over the continental shelf (Al-Abdessalaam, 1995; Randall, 1995). Conversely, the bottlenose dolphin that stranded in the Muscat capital area had primarily eaten

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Table 3. Percentage similarity (PS) values for fish prey species between bottlenose dolphin stomachs that were analysed and between Indo-Pacific humpback dolphin stomachs that were analysed.

PS values for bottlenose dolphin samples							
Sample number	26-05-01-03	29-09-01-05	29-09-01-06	04-10-01-01	01-11-01-01	05-11-01-01	15-02-06-01
26-05-01-03							
29-09-01-05	0.0						
29-09-01-06	0.0	15.4					
04-10-01-01	0.0	15.5	0.0				
01-11-01-01	36.4	24.5	0.0	0.0			
05-11-01-01	20.0	46.2	0.0	4.0	61.1		
15-02-06-01	0.0	0.0	2.5	0.0	0.0	0.0	
02-05-06-01	0.0	0.0	0.0	0.0	0.0	0.0	0.0

PS values for indo-pacific humpback dolphin samples				
Sample number	16-12-01-01A	16-12-01-05A	29-12-01-05	29-12-01-06
16-12-01-01A				
16-12-01-05A	14.3			
29-12-01-05	0.0	0.0		
29-12-01-06	33.3	14.3	66.7	
24-02-06-02	0.0	0.0	0.0	0.0

scombrids, which is a family of pelagic and epipelagic fish (Nelson, 1994). Both cephalopod families found in the stomachs of the Gulf of Masirah bottlenose dolphins are typically found nearshore and over continental shelf waters. However the Sepiidae are primarily demersal while Loliginidae are primarily neritic (Jereb & Roper, 2005).

The findings in the stomach contents of bottlenose dolphins suggest that this species tends to exploit the upper 200 m for food in a wide variety of habitats. The relatively high number of apogonids and the cuttlefish *Sepia pharaonis*, and high variety of other reef-associated fish species such as *Terapon jarbua* and *Scomber japonicus* in the diet of Gulf of Masirah dolphins suggest that those dolphins may have favoured areas around coral reefs (Al-Abdessalaam, 1995). Additionally, their diet also comprised species such as the croaker *Otolithes ruber*, that occur on sandy and muddy substrates (Al-Abdessalaam, 1995), which is consistent with the environment in the northern portion of the Gulf of Masirah where most of the bottlenose dolphin specimens were found. This shallow sheltered area and the adjacent central part of the Gulf of Masirah, is highly productive and food is unlikely to be scarce (Banzon *et al.*, 2004). Most fish species consumed by the dolphins that stranded in the Gulf of Masirah were diurnal (Al Abdessalaam, 1995; Randall, 1995). However, the occurrence of several nocturnal and benthopelagic species in those stomachs suggest that the dolphins hunted during both day and night, perhaps in concert with circadian migrations of fish to and from the surface. The purely piscivorous diet of mostly larger, pelagic scombrids, all of which are diurnal species (Al-Abdessalaam, 1995), suggests that the dolphin that stranded in Muscat had fed during the day probably in deeper waters.

Demersal, soniferous fish families, such as Sparidae and Sciaenidae form the dietary basis for bottlenose dolphins in the Pacific region (Walker, 1981; Barros & Wells, 1998). Similarly, sciaenids appeared to be important in the diet of bottlenose dolphins found stranded in the Gulf of Masirah, while sparids were also found in their food items. Five of the nine fish families consumed by offshore bottlenose dolphins in Hong Kong were represented in the stomach contents of the Gulf of Masirah bottlenose dolphins (i.e. Apogonidae, Carangidae, Trichiuridae, Sparidae and Serranidae). Additionally, there were three genera (i.e. *Apogon*, *Trichiurus*

Table 4. Percentage number and percentage frequency of occurrence of fish families and species found in stomachs of Indo-Pacific humpback dolphins. IRI, index of relative importance; n_s, total number of stomachs containing prey items.

Prey species	N	% number	F	% frequency	Modified IRI
Family Ariidae	4	30.8	1	20.0	615.4
Arius sp.	4	30.8	1	20.0	615.4
Family Sciaenidae	7	53.8	5	100.0	5385.0
Johnius sp.	3	23.0	2	40.0	923.2
Otolithes ruber	3	23.0	3	60.0	1384.8
Unidentified sciaenid	1	7.7	1	20.0	153.8
Family Synodontidae	2	15.4	1	20.0	307.6
Saurida undosquamis	2	15.4	1	20.0	307.6
Total	13	100.0	$n_s = 5$		

Table 5. Percentage number and percentage frequency of occurrence of fish and cephalopod families and species found in stomachs of spinner dolphins. n_s, total number of stomachs containing prey items. Modified index of relative importance not calculated due to small sample size.

Prey species	N	% number	F	% frequency
Fish				
Family Apogonidae	1	0.05	1	50.0
Apogon semiornatus	1	0.05	1	50.0
Family Gempylidae	8	0.4	1	50.0
Neoepinnula orientalis	8	0.4	1	50.0
Family Myctophidae	2165	99.4	2	100.0
Benthosema pterotum	2165	99.4	2	100.0
Family Nomeidae	1	0.05	1	50.0
Cubiceps pauciradiatus	1	0.05	1	50.0
Unidentified sp. 1	4	0.2	1	50.0
Fish totals	2179	100.0		
Cephalopods				
Family Onychoteuthidae	23	100.0	2	100.0
Onychoteuthis banksi	23	100.0	2	100.0
Total	2202	100.0	$n_s = 2$	

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and *Epinephelus*) and one species of fish (i.e. *Trichiurus lepturus*) that offshore bottlenose dolphins in both Hong Kong and the Gulf of Masirah had consumed in common (see Barros *et al.*, 2000). Of the 34 fish families found in the stomach contents of Indo-Pacific bottlenose dolphins in Zanzibar, eight were also represented in the stomach contents of the Gulf of Masirah dolphins, while there were four genera (i.e. *Apogon*, *Carangidae*, *Gerres* and *Saurida*) in common between the two populations. Additionally, only one (Apogonidae) of those eight families was important for dolphins from both areas. In India, the stomach of a bottlenose dolphin also contained predominantly sciaenids (Natarajan & Rajaguru, 1985).

The lack of similarity in the stomach contents of all the Gulf of Masirah specimens and the Muscat specimen may be a reflection of the presence of two species of bottlenose dolphins (*T. aduncus* and *T. truncatus*) in Oman occupying two different habitats. Although tissue samples for genetic analysis and cranial material for taxonomic measurements were routinely collected when available and feasible, other factors, including sample degradation and the absence of cranial remains, precluded identification of carcasses to species level. Bottlenose dolphin specimens used here were typically in either advanced stages of decomposition or located on very remote beaches with little opportunity for collection of skeletal remnants. Nonetheless photographs and observations of live sightings of bottlenose dolphins during small-boat surveys in the Gulf of Masirah between 2000 and 2006 suggest that it is most likely that *T. aduncus* inhabits the shallow waters (mostly in depths of less than 20 m) of this large bay. Individuals had estimated body lengths of less than 3 m, had slender rostra, prominent ventral spotting and physically resembled *T. aduncus* as described in Wang *et al.* (2000) (Ponnampalam, 2009; Minton *et al.*, 2010). Those sighting depths were consistent with the reported preferred depth of *T. aduncus* (Findlay *et al.*, 1992; Wells & Scott, 2002). The dolphin found stranded in Muscat was also less than 3 m long. However, it was the largest of all bottlenose dolphins examined in this study and at 2.75 m length (Table 1), exceeded the maximum recorded length of *T. aduncus* as reported by Wang *et al.* (2000). We consider it likely that this specimen, which was more robust, stocky and blunt-nosed, was a *T. truncatus*. Its diet, consisting mainly of a variety of pelagic tuna, reflects that it was almost certainly feeding off the Muscat coast. There the continental shelf is narrow, depths greater than 200 m can be found within 10 km from shore (Figure 1) and fishermen are often seen hand-lining for yellowfin and longtail tuna within 5 km of the coast. Examination of its mouth showed that all teeth were erupted, though not worn, a sign that the dolphin was a sub-adult, and could possibly attain more than 3 m in length when fully grown. Ponnampalam (2009) and Minton *et al.* (2010) have previously reported that bottlenose dolphins sighted in the Muscat region are stocky, blunt-nosed and heavily scarred, some of which had estimated body lengths exceeding 3 m and resembled *T. truncatus*.

Skin samples taken from these dolphins await genetic analyses for confirmation of species-level identification. Until then, no definitive conclusions can be made on their taxonomic identity.

INDO-PACIFIC HUMPBACK DOLPHINS

The prey spectrum of Indo-Pacific humpback dolphins examined here appeared to be small in comparison to bottlenose dolphins and to consist mainly of coastal, inshore species that inhabit murky waters with muddy substratum. The croaker *Otolithes ruber* is a benthopelagic sciaenid species found in relatively shallow and turbid waters (Al-Abdessalaam, 1995). The other genus of sciaenid represented in the stomach contents was *Johnius*. Randall (1995) reports four species of *Johnius* to occur in Omani waters, all of which are demersal, coastal species (Sasaki, 2001). The otoliths of sea catfish (Ariidae) that were found in one of the stomachs were too degraded to enable species-level identification. Randall (1995) reported that sea catfish in Oman are represented solely by the genus *Arius* in four different species. All four species are demersal, and mostly occur in shallow inshore, rocky and muddy waters. Dead ariids floating at the surface, likely to be fishing discards, were often encountered during small-boat surveys in the Gulf of Masirah (Ponnampalam, 2009).

Baldwin *et al.* (2004) showed a clustering of live sightings of Indo-Pacific humpback dolphins in the Ghubhat Hashish, a semi-enclosed and shallow bay located in the northern reaches of the Gulf of Masirah, particularly in the areas around Mahawt Island and Khaluf, where groups of up to 50 animals were observed. Four of the five Indo-Pacific humpback dolphins examined in this study were found on the beach of Khaluf (see Figure 1). Acoustic watches conducted for cetaceans during small-boat surveys in the Gulf of Masirah, particularly at stations situated between Khaluf and Barr al Hikman, also yielded a variety of grunts and croaks typical of soniferous fish species such as *O. ruber* and *Johnius* sp. (Al-Abdessalaam, 1995). The sciaenids found in the Indo-Pacific humpback dolphin stomachs had the two highest values of modified IRI of all the prey species found. It is thus likely that the Gulf of Masirah, which is characterized by very shallow (10 m), murky waters, particularly in the northern portion where Indo-Pacific humpback dolphins are frequently sighted and occur in large groups, is a rich source of food and provides important feeding grounds for this species—direct observations of feeding activity in the area further support this notion (Baldwin *et al.*, 2004).

In this study, although the sample size was small and prey species diversity was low, the Oman Indo-Pacific humpback dolphins showed some similarity in their mainly piscivorous diet to other conspecifics. One study of stomach contents from eight dolphins in Hong Kong revealed that 81% of the almost entirely piscivorous diet was based on the families Sciaenidae, Engraulidae and Clupeidae (Jefferson, 2000). Another Hong Kong study reported that the dolphins consumed trichiurids and ariids (Barros *et al.*, 2004). In southern China, Indo-Pacific humpback dolphins were also found to be preying mainly upon estuarine fish species (Wang, 1995). Sciaenid fish were important to the Indo-Pacific humpback dolphins in both Hong Kong and Oman. There were two prey genera in common between the dolphins in this study and those from Hong Kong, one of which (*Johnius*) was numerically important for both populations. The Indo-Pacific humpback dolphins in Xiamen Harbor, southern China, had also consumed fish of the genus *Johnius* (Wang, 1995). Conversely, in India, an Indo-Pacific humpback dolphin incidentally caught in gill nets was found to have consumed only teleost fish, although none of these were sciaenids or ariids (Krishnan *et al.*, 2007). Finding marine catfish in the stomachs of humpback dolphins in this study is interesting to note. Barros *et al.* (2004) pointed out that the catfish are a 'bottom-dwelling species possessing dangerous spines

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covered by a venomous mucus, capable of inflicting lacerating wounds' (Smith & Heemstra, 1986). Given the apparent abundance of ariids in Oman, the dolphins may have adapted a way to digest or avoid their venomous, spiny prey without harming their stomachs and internal organs, taking advantage of a possibly abundant food resource.

Spinner dolphins

Myctophids, the primary prey items of both spinner dolphin specimens examined here, are common and occur throughout most of the world's oceans (Dalpadado & Gjøsaeter, 1988; McClatchie & Dunford, 2003). The Myctophidae is a family of fish known to undertake daily vertical migrations from bathypelagic (1000–4000 m) and mesopelagic (200–1000 m) depths during the day, to depths of 200 m up to the surface during the night (Clarke, 1973; Paxton & Hulley, 1999). A survey in 1990 in the Sea of Oman by the RV 'Rastrelliger' found that myctophids were most abundant off the Al Batinah coast (Johannesson, 1995), where the two spinner dolphins examined in this study had been found stranded.

Gjøsaeter (1984) and Johannesson (1995) reported the myctophid *Benthosema pterotum* to be the most abundant and dominant mesopelagic species in the Sea of Oman. *Benthosema pterotum* was also the only mesopelagic species found in the vicinity of a fixed station in the Sea of Oman (Sætersdal *et al.*, 1999). Another species found in the stomachs of the spinner dolphins was the bathypelagic nomeid *Cubiceps pauciradiatus*. It inhabits water depths between 58 and 1000 m but is found near the surface at night (Butler, 1979). This species only contributed 0.4% in number among the stomach contents, and may have been dispersed in the dense schools of *B. pterotum* near the surface. The gempylid *Neoepinnula orientalis* is found between 200 and 570 m depth (Nakamura & Parin, 1993). It is not known if *N. orientalis* undertakes vertical migration towards the shallower depths at night although some species of Gempylidae do (Nakamura & Parin, 1993). *Apogon semiornatus* is an inshore species that occurs on rocky or rubble reef, and by day has a preference for caves. It is found at 5–30 m depth (Heemstra, 1995). Though not typically reported in the diet of spinner dolphins, apogonids have been found in their stomach contents by studies elsewhere (Perrin & Gilpatrick, 1994).

Fitch & Brownell (1968) suggested that spinner dolphins feed at depths greater than 250 m. Dolar *et al.* (2003) hypothesized that this species may feed as deep as 400 m. However, spinner dolphins in the Philippines were observed feeding near the surface at night (Dolar *et al.*, 2003). The high density of myctophids near the surface at night in the Sea of Oman (Gjøsaeter, 1984; Valinassab *et al.*, 2007) coupled with their high abundance in the dolphins' stomachs suggest that the spinner dolphins examined here are likely to have fed mainly in the epipelagic layer at night. Although spinner dolphins were observed frequently in association with schools of feeding yellowfin tuna (*Thunnus albacares*) in the day during detailed behavioural studies off Muscat, feeding was rarely observed (only 3% of total observation time) (Ponnampalam, 2009).

The diet of spinner dolphins has been studied extensively in the Eastern Tropical Pacific (ETP) and in the Hawaiian archipelago. Fitch & Brownell (1968) examined the stomachs of five spinner dolphins caught in the ETP and found a mainly piscivorous diet comprising 6–15 species in eight families, whereby the myctophids *B. panamense* and *Lampanyctus parvicauda* constituted 50% of the dolphins' diet. Squid predominated in the stomach contents of a single dolphin caught in Hawai'i, although there were also fish from the families Gempylidae and Myctophidae (Shomura & Hida, 1965). Dolar *et al.* (2003) examined the stomachs of 45 spinner dolphins that had been caught in the tuna driftnet fishery in the Sulu Sea and found that myctophids formed the basis of the dolphins' diet (32 species, 94% in occurrence), with three species dominating. Furthermore, 10 families of mesopelagic cephalopods, dominated by the family Enoploteuthidae, and crustaceans from three families (Oplophoridae, Penaeidae and Sergestidae) were also found in the stomachs (Dolar *et al.*, 2003).

The stomach contents of the Oman spinner dolphins had a much lower diversity (five fish and one cephalopod species) than those in the ETP and the Philippines. However, as in the Sulu Sea, Hawai'i and ETP, mesopelagic fish, particularly myctophids dominated the stomach contents. The genus *Benthosema* was important for both ETP dolphins and the ones in this study, while the squid *O. banksi* was a prey item of both Sulu Sea spinner dolphins and the spinner dolphins from this study. In contrast, in two separate studies in India, examination of the stomach contents of two spinner dolphins caught incidentally in gill nets revealed that one animal had mainly consumed the epipelagic scad mackerel *Megalaspis cordyla* (Karbhari *et al.*, 1985), while the other had mostly taken shallow water pandalid prawns and the squid *Loligo duvaucelli* (Natarajan & Rajaguru, 1985), while in yet another study in India, a spinner dolphin caught incidentally was found to have consumed mainly the shrimp *Solenocera crassicornis*, also found in shallow water (Krishnan *et al.*, 2007). Two possible reasons for the low diversity in the stomach contents examined here are the extremely small sample size, lacking representation from what could be a larger prey spectrum and/or over-representation of a single species of mesopelagic fish (*B. pterotum*) in the Sea of Oman (Gjøsaeter 1984; Valinassab *et al.*, 2007).

Commercial importance of prey species

Of the 22 prey species found in the stomachs of bottlenose dolphins, only a few are of major commercial importance in Oman, being targeted either by traditional or industrial fishers, or both (Al-Abdessalaam, 1995). Apogonidae, the most important prey family numerically for bottlenose dolphins has no commercial value in Oman (Al-Abdessalaam, 1995). *Otolithes ruber*, important to both bottlenose and Indo-Pacific humpback dolphins, contributes significantly to the overall croaker fishery in Oman (Al-Abdessalaam, 1995; Ministry of National Economy, 2007). In 1995, trichiurids ranked among the top five families in the Omani demersal fish catch, along with sciaenids, siganids, serranids and lethrinids (Siddeek *et al.*, 1999). *Arius* spp., consumed by Indo-Pacific humpback dolphins, is caught commercially in bottom trawlers, although not highly valued as a food fish in Oman, and thus are mostly discarded due to the lack of local demand (Al-Abdessalaam, 1995). Mesopelagic species in the Sea of Oman, particularly the dominant *Benthosema pterotum*, remain a largely unexploited fisheries resource, thus providing the potential for developing a fishery for fishmeal (Gjøsaeter, 1984; Johannesson, 1995). Al-Marzooqi

(2001) reported that the abundance of myctophids in the Gulf of Oman and Arabian Sea has sparked interest in developing a fishmeal fishery in the area. However, Valinassab *et al.* (2007) reported that maximum yields of *B. pterotum* in the Sea of Oman, which undergo seasonal fluctuations, would not be adequate for sustaining the fishery. More research is needed on the consumption biomass of spinner dolphins in Oman to be able to discern whether a myctophid fishery would have impacts on their feeding ecology.

LIMITATIONS OF THIS STUDY

As discussed above, small sample sizes may lead to biases associated with lack of the full range of prey species or over-representation of species comprising the last few meals of the few animals examined. Further limitations pertaining to this dataset include the lack of availability of relevant allometric coefficients to conduct length and weight regressions. This prevented percentage by weight (%W) and passage time analyses. Additionally, the identification of cephalopod beaks may not be entirely accurate for several reasons. Firstly, all published references for Oman, including those of the Ministry of Agriculture and Fisheries (currently known as Ministry of Agriculture and Fisheries Wealth) indicate that *Sepia pharaonis* and *Octopus aegina* are the only cephalopod species to occur in Oman. Published information on cephalopod diversity for the wider region is also scant and there was no readily available reference collection of beaks or a suitable beak identification key for Oman or surrounding waters.

Possible sources of bias in the data

There are biases associated with studying diet based on stomach contents of beach-cast cetaceans. For example, the dolphins in this study were found in varying states of decomposition and with varying states of stomach fullness. Their causes of mortality could not always be determined, and in some cases might have been due to illness or by-catch. If the samples had come from sick individuals, samples used here may not be completely reflective of a normal diet in a healthy dolphin. In the case of by-catch, dolphins are sometimes known to regurgitate some or all of their stomach contents upon capture or entanglement in the fishing gear, perhaps due to stress (e.g. Sekiguchi *et al.*, 1992; Krishnan *et al.*, 2007). If some of the stomachs studied here were from by-caught dolphins, then the results may also not be truly representative of their actual diet, as they may have been feeding opportunistically near fishing vessels or off fishing gear prior to incidental capture. There are also biases associated with the digestibility of prey items. For instance, larger and denser fish otoliths tend to be retained intact for longer than smaller otoliths (Murie & Lavigne, 1985), due to their differing rates of erosion (Jobling & Breiby, 1986). It is thus possible that the results here over-represent fish species with larger otoliths and under-represent fish species with smaller and more fragile otoliths. It also does not necessarily indicate that all prey species found in each stomach were taken in a single meal. Another bias resulting from stomach contents analysis is the longer retention of cephalopod beaks within the stomach compared with fish otoliths (Heezik & Seddon, 1989). However, this bias is likely not to have affected the results here as most samples examined in this study contained more otoliths than beaks. Some of the prey remains found could have been secondary prey items (i.e. prey consumed by the dolphin's prey), thus potentially biasing results. Additionally, due to small sample size and lack of life history data for examined specimens, it was not possible to examine the diet and prey selection of each dolphin based on sex, maturity or seasonality. Several studies have found dietary differences at varying stages of maturity and life history due to demographic differences in habitat selection and/or ontogenetic changes in prey choice, between sexes and between seasons (Robertson & Chivers, 1997; Amir *et al.*, 2005; Santos *et al.*, 2007).

CONCLUSIONS

While the stomach contents data indicate that bottlenose dolphins and Indo-Pacific humpback dolphins in the Gulf of Masirah are feeding in overlapping habitats, the results also indicated that the two species have different prey spectra with only minor overlaps in species consumed. Spinner dolphins were more specific in their prey choice and were able to exploit what appears to be an abundant food resource from the vertically migrating mesopelagic deep-scattering layer. Only a small percentage of the three dolphin species' prey items are of current commercial importance, indicating that there is little direct competition with local fisheries. However, a number of animals examined in this study showed signs of mortality due to fisheries interaction, indicating that these dolphins still face a significant risk of incidental capture from feeding in the same highly productive areas where fishing occurs. Despite the limitations of this study, the data presented here remain important in furthering our understanding of the ecology of small cetaceans in this region and for designing future studies on this subject.

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