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Comparative Analysis of the Diets of Pygmy Sperm Whales and Dwarf Sperm Whales in Taiwanese Waters

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ABSTRACT

Stomach contents were analyzed of six pygmy sperm whales (*Kogia breviceps*) and five dwarf sperm whales (*Kogia sima*) which were taken as by-catch or were stranded specimens in coastal Taiwan from 1998 through 2000. Twenty-two species in 12 families of oceanic cephalopods were identified. In pygmy sperm whales, *Enoploteuthis chunii*, *Sthenoteuthis oualaniensis*, and *Taonius pavo* were the primary prey in the diet, while *E. chunii*, *Histioteuthis miranda*, and *T. pavo* were the most important prey items ingested by dwarf sperm whales. Although the primary prey items these two species ingested were very similar, each item comprised a different proportion for each whale species. A similarity test demonstrated a significant difference in prey composition, and SIMPER analysis showed that *E. chunii* was ranked first and contributed 37.1% to the average dissimilarity between pygmy and dwarf sperm whales. Pygmy sperm whales fed on much larger *T. pavo* compared to those ingested by dwarf sperm whales, while dwarf sperm whales ingested more *H. miranda* than did pygmy sperm whales. These results support the view that pygmy sperm whales live seaward of the continental shelf and that dwarf sperm whales live more in coastal waters.

Key words:*Kogia*, *Enoploteuthis chunii*, cephalopod, stomack contents

INTRODUCTION

Pygmy (*Kogia breviceps*) and dwarf sperm whales (*Kogia sima*) occur in tropical and temperate latitudes worldwide. They are generally sighted in waters over the continental shelf and slope in eastern Taiwan (Yeh, 2000). Several studies have indicated that pygmy sperm whales live mostly beyond the edge of the continental shelf, while dwarf sperm whales inhabit the shelf-edge and slope waters (e.g., Rice, 1998).

Several studies have reported the stomach

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contents of stranded *Kogia* species, i.e., from South Africa (Sekiguchi *et al*., 1992) and south-eastern and southern Brazil (Santos and Haimovici, 2001). These reports showed that most of the stomach contents of *Kogia* species are oceanic cephalopods, with *Histiotuethis* spp. dominating the diets, with only a few remains of fishes and crustaceans being found (Sekiguchi *et al*., 1992; Santos and Haimovici, 2001). Stranded animals are often used for diet analyses, but they are usually unhealthy and have fewer stomach contents (Jones, 1981) than do non-stranded animals, and may have different prey compositions (Leatherwood *et al*., 1978) in their stomachs; therefore, they might not provide data representative of normal diets.

The beaks of cephalopod remains in stomach contents are usually in a condition where identification to family, genus, and often species is possible, and estimations from beak size can be made of their relative contribution to the diet by weight and number of various taxa (Clarke, 1986). This is not only important for dietary analysis, but also informative with respect to the distribution and relative abundance of the various cephalopod taxa in the sea, because many of the cephalopods eaten by oceanic cetaceans are rarely caught in nets (Clarke, 1986).

Little is known about the stomach contents of *Kogia* species from Taiwanese waters. The present collections of the stomachs of two *Kogia* species were from stranded and by-caught specimens. The aim of this paper was to provide the first dietary information for pygmy and dwarf sperm whales from Taiwanese waters. This study also presents a qualitative description of the diet, and the relative importance of prey species assessed through frequency of occurrence, as well as numerical and biomass indices.

MATERIALS AND METHODS

Sample collection

Six and five stomach samples were collected from by-caught and stranded specimens of pygmy and dwarf sperm whales, respectively, from the west and east coasts of Taiwan, during 1998 through 2000. Stomachs were tied off at the esophageal and pyloric ends prior to being removed intact from the animal. Each stomach was tagged with an individual specimen number and stored in a freezer. Data of each cetacean individual, including its length and sex, were collected in port. In the laboratory, stomachs were thawed overnight at room temperature prior to preliminary sorting and specimen preservation. The stomach of each specimen was weighed full and empty to the nearest 0.1 g with an A&D GF-6000 balance.

In the laboratory, the contents of each stomach were carefully removed, separated into identifiable components, and drained of excess fluid. The stomach lining was thoroughly rinsed into a shallow tray and then through a series of sieves with mesh sizes of 1.4 and 0.5 mm, and 500 ìm in order to recover all isolated cephalopod beaks. Dorsal mantle length and weight of the cephalopod prey that were whole or nearly whole were recorded, and the beaks were extracted from the intact prey and saved as reference material for species identification. The cephalopod beaks were sorted and preserved in 70% ethanol.

Prey identification and enumeration

Cephalopod beaks were identified using the private reference collection of W. A. Walker and from illustrations and keys presented in Clarke (1986). The maximum number of upper or lower beaks was used to estimate the minimum number of cephalopods ingested. The relative importance of prey species was evaluated by means of the frequency of occurrence and the percentage by number (Hyslop, 1980).

Estimation of prey size

Estimations of the original dorsal mantle length (DML) and weight of the commonly oc-

curring prey were based on measurements of lower beak rostral length (LBRL). The LBRL was measured to the nearest 0.01 mm with vernier calipers or an optical micrometer. Damaged or eroded specimens were not measured. The DML and weight of *Enoploteuthis chunii* were estimated using equations developed from intact specimens in stomach contents. Regression equations for other cephalopod prey were from Clarke (1986). When identification to species level was not possible, cephalopod weight and length were estimated by using regressions available for the genus or family.

Comparative analysis

Non-parametric multivariate techniques were used to compare differences between the diets of the pygmy and dwarf sperm whales. The computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research) was used in the analysis. The data were put into triangular matrices based on Bray-Curtis similarities. An ANOSIM permutation test was performed to test the null hypothesis that there were no differences between species. It is based on a non-parametric permutation procedure and is applied to the ranked similarity matrix underlying the classification or ordination of samples. Randomization tests for significance were used for *a priori* selection by comparing the ranked similarities of samples between and within species. ANOSIM derives a test statistic, R, from a matrix of ranked similarities between all replicate samples, which represents the degree of difference between seasons or species. In theory, R can take any value between 1 and –1, and R = 1 if all replicate samples within a species are more similar to each other than to any samples from other species, while an *R* value of 0 indicates that within group similarities are, on average, equal to between-species similarities. Another technique (Similarity Percentages, SIMPER) was used to reveal the percentage contributions of each taxon to the average dissimilarity between the two *Kogia* species. The mean contribution of each species to the dissimilarity of two clusters is defined as an average overall cross-group pair of samples. This yields an assessment of which prey species are diagnostic species between the two *Kogia* species.

RESULTS

Both pygmy sperm whales and dwarf sperm whales fed on oceanic squid. Muscular squid comprised more than 60% of the diets of these two *Kogia* species, both numerically and on a weight basis (Table 1). Cephalopods ingested were neutrally buoyant squid such as *Histioteuthis miranda* and *Taonius pavo* which amounted to 30% of the specimens eaten and muscular squids like *Enoploteuthis chunii* and those of the Ommastrephidae which comprised 70%. For both species of whales, *E. chunii* and *T. pavo* made up about 70% of the total number of prey items ingested. They were also the important prey on a weight basis.

***Kogia breviceps* (Pygmy sperm whale)**

Eighteen species in nine families of squids were identified by beaks or undigested remains. The enoploteuthid squid, *E. chunii*, was the primary prey, representing 48.6% of the total prey counts, with an overall occurrence of 50.0%. The cranchiid squid, *Taonius pavo*, ranked second and made up 18.9% of the total number of prey ingested, with an overall occurrence of 33.3%. The ommastrephid squid, *Sthenoteuthis oualaniensis*, was the third most abundant prey item and represented 5.4% of the total number of prey items, with an occurrence of 66.7% (Table 2). The squids eaten were small to large sized, the estimated mantle length of the prey ranged from 48.6 to 490.2 mm, and the weight ranged from 14.8 to 1186.3 g (Table 3).

Sthenoteuthis oualaniensis was the most im-

Table 1. Percentage of number (N) and weight (W) of muscular and neutrally buoyant squid in the diets of pygmy and dwarf sperm whales

	Pygmy sperm whale		Dwarf sperm whale	
Type	N%	W%	N%	W%
Muscular	65.7%	63.2%	74.0%	60.3%
Neutrally buoyant	34.3%	36.8%	26.0%	39.7%

Table 2. Occurrence (F), number (N), and estimated total weight (W) for prey recovered from pygmy (n = 6) and dwarf sperm whales (n = 5), from coastal Taiwan.

	Pygmy sperm whale (*Kogia breviceps*)						Dwarf sperm whale (*Kogia sima*)					
Cephalopod species	F	F%	N	N%	W	W%	F	F%	N	N%	W	W%
Enoploteuthidae												
Enoploteuthis chunii	3	50.0	180	48.6	5385.0	14.5	3	60.0	72	58.5	211	38.4
Ancistrocheiridae												
Ancistrocheirus lesueurii	1	16.7	2	0.5	585.2	1.6	-	-	-	-	-	-
Octopoteuthidae												
Octopoteuthis sp.	1	16.7	2	0.5	458.7	1.2	-	-	-	-	-	-
Octopoteuthis sp. cf *O. deletron*	1	16.7	6	1.6	1342.3	3.6	-	-	-	-	-	-
Onychoteuthidae												
Moroteuthis loennbergi	2	33.3	11	3.0	2254.0	6.1	1	20.0	1	0.8	38.8	0.7
Onychoteuthis banksii	1	16.7	2	0.5	384.1	1.0	3	60.0	3	2.4	257.	4.7
Lepidoteuthidae												
Pholidoteuthis boschmai	2	33.3	5	1.4	3218.4	8.7	-	-	-	-	-	-
Histioteuthidae												
Histioteuthis hoylei	3	50.0	7	1.9	1255.6	3.4	-	-	-	-	-	-
Histioteuthis miranda	2	33.3	17	4.6	2443.1	6.6	1	20.0	13	10.6	149	27.2
Histioteuthis reversa	3	50.0	6	1.6	325.1	0.9	-	-	-	-	-	-
Ommastrephidae												
Eucleoteuthis luminosa	3	50.0	4	1.1	213.5	0.6	3	60.0	4	3.3	259.	4.7
Ornithoteuthis volatilis	3	50.0	13	3.5	1599.6	4.3	1	20.0	3	2.4	308.	5.6
Sthenoteuthis oualaniensis	4	66.7	20	5.4	9795.5	26.4	1	20.0	1	0.8	122.	2.2
Ctenopterygidae												
Ctenopteryx sicula	-	-	-	-	-	-	1	20.0	1	0.8	30.6	0.6
Ctenopteryx sp.	-	-	-	-	-	-	1	20.0	6	4.9	184.	3.3
Cycloteuthidae												
Discoteuthis sp.	1	16.7	2	0.5	284.1	0.8	1	20.0	1	0.8	113.	2.1
Mastigoteuthidae												
Mastigoteuthis hjorti	5	83.3	17	4.6	1065.8	2.9	-	-	-	-	-	-
Chiroteuthidae												
Chiroteuthis sp cf *C. veranyii*	1	16.7	1	0.3	99.2	0.3	-	-	-	-	-	-
Cranchiidae												
Taonius pavo	2	33.3	70	18.9	6097.9	16.4	2	40.0	14	11.4	544.	9.9
Galiteuthis armata	-	-	-	-	-	-	1	20.0	2	1.6	13.4	0.2
Leachia dislocata	-	-	-	-	-	-	2	40.0	2	1.6	17.1	0.3
Teuthowenia sp.	2	33.3	5	1.4	291.6	0.8	-	-	-	-	-	-
Total	18		361				13		123			

Notes: F%, the percentage of non-empty stomachs that contained a particular category of prey; N%, the percentage of total number of prey consumed; W%, percentage by weight.

portant prey on a weight basis for the pygmy sperm whale, representing 26.4% of the total weight in the stomach contents. The estimated length frequency of *S. oualaniensis* ranged in size from 164.8 to 305.3 mm in dorsal mantle length with a mean length of 233.5 mm. Estimated weights for *S. oualaniensis* ranged from 158.5 to 1071.1 g with a mean weight of 489.8 g (Table 3).

***Kogia sima* (Dwarf sperm whale)**

Thirteen species in seven families of squid were identified by beaks or undigested remains. The enoploteuthid squid, *E. chunii*, was the primary prey and represented 58.5% of the total prey counts, with an overall occurrence of 60.0%. The cranchiid squid, *T. pavo*, ranked second and made up 11.4% of the total number of prey items ingested, with an overall occurrence of 40.0%. The histioteuthid squid, *H. miranda*, was the third most abundant prey item and represented 10.6% of the total number of prey items, with an occurrence of 20.0% (Table 2). The squid eaten were small to medium sized, with estimated mantle lengths ranging from 30.4 to 348.3 mm and weights ranging from 5.3 to 175.5 g (Table 3).

Enoploteuthis chunii was the most important prey on a weight basis for dwarf sperm whales, representing 38.4% of the total weight of stomach contents. The estimated length frequency of *E. chunii* ranged in size from 56.3 to 88.4 mm in dorsal mantle length with a mean length of 71.3 mm. Estimated weights for *E. chunii* ranged from 15.1 to 51.9g with a mean weight of 29.4 g (Table 3).

Comparative analysis

In total, 22 taxa were identified in this study. The data matrices were standardized and analyzed by ANOSIM test, which demonstrated a significant difference ($R = 0.25$, $p < 0.05$) between the pygmy and dwarf sperm whale samples. The SIMPER analysis identified eight prey species that contributed greater than 90% of the dissimilarity between the two *Kogia* species; they were *E. chunii, T. pavo, M. hjorti, S. oualaniensis, H. hoylei, Eucleoteuthis luminosa, Onychoteuthis banksii,* and *H. miranda* (Table 4). The enoplotheuthid squid, *E. chunii* ranked first and contributed 37.1% to the average dissimilarity.

DISCUSSION

This paper presents new dietary information for Taiwanese waters by comparing differences in stomach contents between by-caught and stranded specimens of pygmy and dwarf sperm whales. Our findings indicate that pygmy and dwarf sperm whales in Taiwanese water feed exclusively on oceanic squid. The squid typically have elaborate luminescent organs, are small to medium in size, school in large numbers, and undergo diel vertical migrations. Sekiguchi et al. (1992) reported that both pygmy and dwarf sperm whales feed on cephalopods of the continental slope and on neutrally buoyant squid. Both species of whales also feed on some hake. Santos and Haimovici (2001) found that the cephalopods eaten were small to medium sized, among which neutrally buoyant squids accounted for 65% of the specimens, while muscular families represented 31%. This report showed no differences in the families of cephalopods eaten by the two *Kogia* species. It is important to examine material from non-stranded animals in order to obtain a more-accurate picture of *Kogia* diets. Our data were collected from both stranded and by-caught specimens, and show that muscular squid comprised more than 60% of the diets of these two species of *Kogia*, both numerically and on a weight basis. Dwarf sperm whales ingested more muscular squid than did pygmy sperm whales (74.0% for dwarf and 65.7% for pygmy sperm whales, on a weight basis). This result contradicts those reported by Sekiguchi *et al.* (1992) and Santos and Haimovici (2001).

Table 3. Number, estimated dorsal mantle length (DML), and body weight (BW) of cephalopods consumed by pygmy (*n* = 6) and dwarf sperm whales (*n* = 5).

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Table 4. SIMPER analysis of cephalopods ingested between pygmy sperm whales (KB) and dwarf sperm whales (KS), with a cut off when the cumulative percent contribution to average dissimilarity reached 90%.

Average dissimilarity = 88.72

Species	Average abundance		Avg. Diss.	Contrib.%	Cum.%
	KB	KS			
E. chunii	30.0	14.4	32.9	37.1	37.1
T. pavo	11.7	2.8	13.1	14.8	51.8
M. hjorti	2.8	0.0	7.9	8.9	60.8
S. oualaniensis	3.3	0.2	7.8	8.8	69.5
H. hoylei	1.2	0.0	5.3	5.9	75.4
E. luminosa	0.7	0.8	4.8	5.4	80.8
O. banksii	0.3	0.6	4.5	5.1	85.9
H. miranda	2.8	2.6	4.4	5.0	90.9

Contrib%, percentage of contribution to dissimilarity; Cum.%, cumulative percentage of contribution dissimilarity; Avg. Diss., average dissimilarity.

Enoploteuthis chunii was one of the most important prey of *Kogia* species. Larval enoploteuthids are most abundant at depths of 100-150 m during the day, and at 30-50 m at night (Young and Harman, 1986). Adults occur at depths of 300-600 m during the day, migrating to the upper 150 m at night (Roper and Young, 1975). Female enoploteuthid squid typically mature at about a dorsal mantle length of 50 mm (Kubota *et al*., 1982; Riddell, 1982). Estimated dorsal mantle length for *E. chunii* in the present stomach samples ranged from 55.9 to 88.4 mm, indicating the *Kogia* species off coastal Taiwan were feeding on adult *E. chunii*. In the coastal waters of Taiwan, *E. chunii* has previously been reported from the stomach of one Cuvier's beaked whale stranded in northwestern Taiwan at Houlong, Miaoli County (Wang *et al*., 1995).

Histiotetuhis miranda is believed to be associated with shallow ocean-floor topography, which occurs near continental slopes, islands, and submarine rises (Voss *et al*., 1998). *Histiotetuhis miranda* was most abundant in water depths of less than 1000 m as indicated by their abundance in the diet of sperm whales (Clarke, 1980). Dwarf sperm whales ingest more *H. miranda* than do pygmy sperm whales (27.2% for dwarf and 6. 6% for pygmy sperm whales, on a weight basis), indicating the more-coastal habitat of dwarf sperm whales in eastern and western Taiwanese waters. This result is consistent with those reported by Rice (1998).

The cranchiid squid, *T. pavo* is also an important prey item in the *Kogia* diet. Young (1975) found its paralarvae in the upper 400 m; juveniles from 50 to 140 mm in dorsal mantle length (DML) were captured at between 500 and 700 m, with most being taken between 600 and 650 m. This species appears to exhibit ontogenetic descent and does not undergo a diel vertical migration (Roper and Young, 1975). The estimated mean DML for *T. pavo* was 309.4 mm in the stomach contents of pygmy sperm whales, which was larger than those ingested by dwarf sperm whales (205.9 mm). These findings suggest that pygmy sperm whales may dive deeper than dwarf sperm whales.

The purpleback flying squid, *S. oualaniensis*

was the most important prey in the stomach of pygmy sperm whales on a weight basis. *Sthenoteuthis oualaniensis* is an oceanic squid widely distributed in the western Pacific and Indian Oceans. *Sthenoteuthis oualaniensis* is scattered at depths ranging from the sea surface down to 200 m at night. The depth of abundance ranged from 50 to 100 m (Siriaksophon *et al*., 2000). The squid remain deeper than 350 m during the day. *Sthenoteuthis oualaniensis* migrates into eastern waters of Taiwan; its fishery production peaks during May to August, and it is used for bait in longline fisheries.

Little is known about cephalopods from the upper slope and open ocean of Taiwanese waters. Many of these offshore cephalopods were absent from former cephalopod surveys (Lu, 1998; 2000). Stomach contents of opportunistic feeders in different geographic regions are likely to reflect the composition of the fish and cephalopod fauna (Young and Cockcroft, 1994). The information obtained from *Kogia* stomach contents can contribute to our knowledge of the oceanic cephalopod fauna of Taiwan. Evidence based on the cephalopod remains in *Kogia* stomach contents suggests that pygmy sperm whales live seaward of the continental shelf. Dwarf sperm whales live over the continental shelf and slope and are somewhat more coastal than pygmy sperm whales.

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台灣海域小抹香鯨及侏儒抹香鯨食性比較

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摘 要

本文分析自1998年至2000年於台灣海岸收集漁業誤捕及擱淺的小抹香鯨6隻、侏儒抹香鯨5隻。大洋性頭足類為其主要的食物，其中包括了12科22種頭足類，另外尚包括了少數十足類。在小抹香鯨的胃內含物中，*Enoploteuthis chunii, Sthenoteuthis oualaniensis*及 *Taonius pavo*是最主要的食物；而侏儒抹香鯨的胃中， *Enoploteuthis chunii, Histioteuthis miranda*及*Taonius pavo*則是最主要的食物。雖然食物相似，但比例不同。利用ANOSIM分析發現小抹香鯨及侏儒抹香鯨的胃中頭足類組成上有明顯差異。在SIMPER分析中，發現小抹香鯨及侏儒抹香鯨之間，*E. chunii*貢獻37.1%的平均相異度。在其主要食物中，小抹香鯨所攝食的*T. pavo*，其平均長度大於侏儒抹香鯨所攝食的，而侏儒抹香鯨則攝食更多的*H. miranda*。此結果支持顯示侏儒抹香鯨的棲地大多在大陸棚及斜坡上，較小抹香鯨更為近岸。

關鍵字: 小抹香鯨科、武裝魷、頭足類、胃內含物