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Feeding Habits of the Pantropical Spotted Dolphin, *Stenella attenuata*, off the Eastern Coast of Taiwan

Ming-Chih Wang[1], William A. Walker[2], Kwang-Tsao Shao[3] and Lien-Siang Chou[1,*]

[1]*Department of Zoology, National Taiwan University, Taipei, Taiwan 106, R.O.C.*
[2]*National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA, USA*
[3]*Institute of Zoology, Academia Sinica, Taipei, Taiwan 115, R.O.C.*

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Ming-Chih Wang, William A. Walker, Kwang-Tsao Shao and Lien-Siang Chou (2003) Feeding habits of the pantropical spotted dolphin, *Stenella attenuata*, off the Eastern coast of Taiwan. *Zoological Studies* **42**(2): 368-378. Stomach contents were analyzed from 45 pantropical spotted dolphins, *Stenella attenuata*, confiscated by Taiwan police and as by-catches by in fisheries off eastern Taiwan from February 1994 to November 1995. Mesopelagic prey species dominated the stomach contents. Sixty-four species of fish made up 67.5% and 21 species of cephalopods made up 32.5% by number. Myctophid lanternfishes and enoploteuthid squid accounted for 78.3% of all prey consumed. The enoploteuthid squid, *Enoploteuthis chunii*, was the primary prey and represented 25.8% by number of the total prey, with an overall occurrence of 66.7%. Results of this study are generally similar to those at earlier food habits studies conducted on this species in the eastern tropical Pacific. In both regions, the ratio of fish and cephalopods consumed and the trophic levels of the dominant prey were similar. *Stenella attenuata* in the eastern tropical Pacific and off the eastern coast of Taiwan are feeding primarily on myctophid lanternfishes and species of the cephalopod families Enoploteuthidae and Ommastrephidae. The ANOSIM analysis demonstrated a significant difference in prey composition by season. The most numerically abundant prey species, *Enoploteuthis chunii*, play an important role in the observed seasonal differences, which contributed 16.8% to the average dissimilarity between fall-winter and spring-summer.
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Key words: *Enoploteuthis chunii*, *Myctophum asperum*, Lanternfish, Otolith, Squid beak.

Cetaceans are exceptional divers and can be excellent collectors of fish and cephalopods (Clarke et al. 1980, Clarke 1986a b).Studies on the diets of cetaceans can contribute to the information on predator-prey relationships in the marine food web ecosystem. Information on prey distribution and habitat can further provide new insights on cetacean distribution, movements, feeding behavior, and trophic relationships. In addition, dietary studies of cetaceans can extend our knowledge of prey species distribution, life history and habitat of the fish and cephalopods they consume (Clarke 1986a, Walker 1996, Silva 1999).

Pantropical spotted dolphins, *Stenella attenuata*, inhabit tropical and warm temperate waters of the world and are one of the most common cetaceans along the eastern Taiwanese coast (Yeh 2000, Chen 2001). Food habits studies of *S. attenuata* have been conducted in other regions of the North Pacific Ocean. These previous studies on the stomach contents of this species reported high number of mesopelagic lanternfish of the family Myctophidae (Fitch et al. 1968, Perrin et al. 1973). However, epipelagic prey was also found to be important and included species of the families Ommastrephidae (flying squid), Onychoteuthidae (hooked squid), and Exocoetidae (flying fish) (Shomura et al. 1965, Fitch et al. 1968, Perrin et al. 1973, Bernard et al. 1989, Robertson et al. 1997). A recent report on the stomach contents of spotted dolphins caught in the eastern tropical

*To whom correspondence and reprint requests should be addressed. Tel: 886-2-23661331. Fax: 886-2-23639902. E-mail: chouls@ccms.ntu.edu.tw

Pacific (ETP) showed that the most common prey fish were lanternfishes (Myctophidae), and the most frequently occurring cephalopods were species of the family Ommastrephidae (Robertson et al. 1997).

Information on feeding habits of *S. attenuata* is lacking in the waters of Taiwan. In this paper, we present a quantitative description of the diet. The relative importance of prey species is assessed through the frequency of occurrence, as well as numerical and biomass indices. Prey size of some of the commonly ingested species is estimated from measurements of otoliths and squid beaks recovered from the stomach contents. Seasonal variability of prey species is also analyzed.

MATERIALS AND METHODS

Sample collection

In total 45 stomach samples were collected from pantropical spotted dolphins confiscated by Taiwan police for being sold illegally and as by-catch specimens at the port of Nanfanao, Ilan County, Taiwan (24°25'N, 121°50'E), from Feb. 1994 through Nov. 1995. Those pantropical spotted dolphin specimens were all from local fisheries. Stomachs were tied off at the esophageal and pyloric ends prior to being removed intact from the animal at the port. Each stomach was tagged with an individual specimen number and placed in frozen storage. Data recorded on each individual cetacean collected included length and sex. Stomachs were thawed overnight at room temperature prior to preliminary sorting and content preservation. The stomach of each specimen was weighed in both its full and empty condition to the nearest 0.1 g.

In the laboratory, stomach contents were carefully removed, separated into identifiable components, and drained of excess fluid. The stomach lining was then thoroughly rinsed into a shallow tray and the residual run through a series of sieves of 1.4-mm, 0.5-mm, and 500-μ mesh sizes in order to recover all isolated fish otoliths, bones, and cephalopod beaks. The standard length of fish, the dorsal mantle length of cephalopods, and weights were recorded for specimens that were whole or nearly whole. Otoliths and beaks were extracted from identifiable, intact specimens and saved as reference material for species identification and development of prey-size regressions. All otoliths, key fish bones and skeletons were placed in dry storage. Key cephalopod remains and beaks were sorted and preserved in 70% ethanol.

Prey identification and enumeration

Because of rapid digestion, identification and enumeration of fish and cephalopod prey species relied almost exclusively on hard remains. Fish otoliths from known species used for comparison in this study were from the John Fitch reference collection at the Los Angeles County Museum of Natural History, Department of Ichthyology, as well as the private collections of W.A. Walker and the senior author. The minimum number of individual fish ingested was determined by the greater number of left or right otoliths.

Cephalopod beaks were identified using the private reference collection of W.A. Walker and from the illustrations and keys presented in Clarke (1986b). 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

Estimation of the original length and weight of the most commonly occurring prey is based on the regression of prey body length in relation to otolith or lower beak rostral length. Otolith lengths were measured to the nearest 0.01 mm using a camera (JVC TK-1270 color video camera) and image processing software (HLImage++97, 1997). The lower beak rostral length of cephalopod beaks was measured to the nearest 0.01 mm with vernier calipers or an optical micrometer. Damaged or eroded specimens were not measured.

The sizes of fish prey were estimated by regression equations of fish length and wet weight on otolith length. Standard length (SL) and weight estimates for *Mytophum asperum* were derived from equations developed from specimens and data maintained in the reference collection of W.A. Walker. Standard length and weight estimates for *Diaphus schmidti*, *D. watasei*, *Decapterus macrosoma*, *Trichiurus lepturus*, and *Scomber australasicus* were derived from regression equations of standard length on otolith length developed from specimens obtained by the senior author from local fisheries in Ilan, northeastern Taiwan. Standard length and weight of *Engraulis japonicus*, *S. japonicus*, and *Lampanyctodes hectoris* were estimated by regression equations presented in Smale (1995).

Cephalopod prey size, and dorsal mantle length and weight were estimated from the lower beak rostral length. Dorsal mantle length (DML) and weight of *Enoploteuthis chunii* were estimated using a regression equation developed from intact specimens in stomach contents. Regression equations of the ommastrephid squid, *Sthenoteuthis oualaniensis*, *Euleoteuthis luminosa*, and the onychoteuthid squid, *Onychoteuthis banksii* were from Clarke (1986b).

Seasonal variation

Samples were pooled into 2 seasons: fall-winter (Oct.-Mar.) and spring-summer (Apr.-Sept.). Non-parametric multivariate techniques used to compare differences between the 2 seasonal biotic communities follow (Clarke 1993). The data were placed 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 seasons (Clarke et al. 1988). Another technique (Similarity Percentages, SIMPER) was used to reveal the percentage contribution of each taxon to the average dissimilarity between samples of each season. The mean contribution of each species to the dissimilarity of the 2 clusters is defined as an average over all cross-group pairs of samples. This yields an assessment of which prey species are diagnostic species between seasons (Clarke 1993). The computer software package PRIMER (Plymouth Routines in Multivariate Ecological Research) was used in the analysis.

RESULTS

Stomach contents were from 24 female and 21 male pantropical spotted dolphins. All 45 stomachs contained prey remains. Sixty-four species of fish and 21 species of cephalopods were identified by fish otoliths, squid beaks, or undigested prey remains. Twenty-five families of fish made up 67.5% of the total number of prey items, with an overall occurrence of 100%. Thirteen families of cephalopods made up 32.5% of the total number of prey ingested, with an overall occurrence of 100% (Table 1).

There were 1 fish family, Myctophidae, and 2 cephalopod families, Enoploteuthidae and

Table 1. Frequency of occurrence and number of prey recovered from pantropical spotted dolphins, *Stenella attenuata*, (n = 45) from the eastern waters of Taiwan

Food item	Occurrence		Number	
	No.	Frequency (%)	No.	Percent of total
Total	**45**	**100.0**	**4281**	**100**
Fish	45	100.0	2890	67.5
Congridae	**2**	**4.4**	**2**	**< 0.1**
Congridae (unidentified)	2	4.4	2	<0.1
Engaulidae	**8**	**17.8**	**133**	**3.1**
Engraulis japonicus	8	17.8	133	3.1
Argentinidae	**3**	**6.7**	**3**	**< 0.1**
Glossanodon semifaciata	3	6.7	3	< 0.1
Alepocephalidae	**1**	**2.2**	**2**	**< 0.1**
Xenodermichthys sp.	1	2.2	2	< 0.1
Gonostomatidae	**4**	**8.9**	**64**	**1.5**
Gonostoma elongatum	3	6.7	63	1.5
Diplophos taenia	1	2.2	1	< 0.1
Sternoptychidae	**13**	**28.9**	**45**	**1.1**
Polyipnus indicus	7	15.6	14	0.3
Polyipnus sp. 1	2	4.4	3	< 0.1
Polyipnus sp. 2	4	8.9	28	0.7
Chlorophthalmidae	**4**	**8.9**	**22**	**0.5**
Chlorophthalmus sp. 1	3	6.7	21	0.5
Chlorophthalmus sp. 2	1	2.2	1	< 0.1

Table 1. (Cont.)

Food item	Occurrence No.	Occurrence Frequency (%)	Number No.	Number Percent of total
Paralepididae	**8**	**17.8**	**12**	**0.3**
Lestidiops similis	1	2.2	2	< 0.1
Lestrolepis intermedia	6	13.3	8	0.2
Paralepis sp.	2	4.4	2	< 0.1
Notosudidae	**1**	**2.2**	**11**	**0.3**
Notosudidae (unidentified)	1	2.2	11	0.3
Myctophidae	**37**	**82.2**	**2131**	**49.3**
Benthosema fibulatum	2	4.4	4	< 0.1
Benthosema panamense	1	2.2	1	< 0.1
Ceratoscopelus warmingii	4	8.9	11	0.3
Diaphus jenseni	2	4.4	3	< 0.1
Diaphus mollis	4	8.9	7	0.2
Diaphus schmidti	21	46.7	564	13.2
Diaphus sp. 1	1	2.2	1	< 0.1
Diaphus sp. 2	1	2.2	2	< 0.1
Diaphus sp. 3	4	8.9	100	2.3
Diaphus sp. 4	2	4.4	2	< 0.1
Diaphus sp. 5	2	4.4	10	0.2
Diaphus watasei	13	28.9	203	4.7
Lampadena luminosa	1	2.2	2	< 0.1
Lampanyctodes hectoris	5	11.1	103	2.4
Lampanyctodes sp.	1	2.2	1	< 0.1
Lampanyctus australis	2	4.4	3	< 0.1
Lampanyctus sp. 1	5	11.1	66	1.5
Lampanyctus sp. 2	4	8.9	25	0.6
Myctophum asperum	19	42.2	871	20.3
Myctophum aurolaternatum	20	44.4	65	1.5
Myctophum nitidulum	5	11.1	9	0.2
Myctophum obtusirostre	7	15.6	24	0.6
Myctophum sp. 1	7	15.6	22	0.5
Myctophum sp. 2	2	4.4	14	0.3
Myctophum sp. 3	1	2.2	1	< 0.1
Myctophum spinosum	1	2.2	5	0.1
Symbolophorus evermanni	5	11.1	6	0.1
Myctophidae (unidentified)	5	11.1	6	0.1
Bregmacerotidae	**3**	**6.7**	**33**	**0.8**
Bregmaceros nectabanus	3	6.7	33	0.8
Exocoetidae	**3**	**6.7**	**6**	**0.1**
Exocoetidae (unidentified)	3	6.7	6	0.1
Belonidae	**3**	**6.7**	**3**	**< 0.1**
Tylosurus acus melanotus	3	6.7	3	< 0.1
Percichthyidae	**3**	**6.7**	**9**	**0.2**
Synagrops japonicus	3	6.7	9	0.2
Acropomatidae	**1**	**2.2**	**2**	**< 0.1**
Malakichthys elegans	1	2.2	2	< 0.1
Serranidae	**1**	**2.2**	**1**	**< 0.1**
Serranidae (unidentified)	1	2.2	1	< 0.1
Priacanthidae	**4**	**8.9**	**17**	**0.4**
Priacanthus macracanthus	4	8.9	17	0.4
Apogonidae	**3**	**6.7**	**19**	**0.4**
Apogon carinatus	3	6.7	19	0.4
Carangidae	**10**	**22.2**	**105**	**2.5**
Decapterus macrosoma	8	17.8	86	2.0
Decapterus maruadsi	3	6.7	6	0.1

Table 1. (Cont.)

Food item	Occurrence		Number	
	No.	Frequency (%)	No.	Percent of total
Decapterus russelli	5	11.1	8	0.2
Decapterus sp.	1	2.2	1	< 0.1
Carangidae (unidentified)	1	2.2	4	< 0.1
Gempylidae	**10**	**22.2**	**59**	**1.4**
Rexea prometheoides	10	22.2	59	1.4
Trichiuridae	**5**	**11.1**	**125**	**2.9**
Trichiurus lepturus	5	11.1	125	2.9
Scombridae	13	28.9	50	1.2
Auxis thazard	1	2.2	1	< 0.1
Scomber australasicus	10	22.2	32	0.7
Scomber japonicus	6	13.3	17	0.4
Stromateidae	**1**	**2.2**	**2**	**< 0.1**
Pampus argenteus	1	2.2	2	< 0.1
Tetraodontidae	**4**	**8.9**	**34**	**0.8**
Lagocephalus sp.	1	2.2	1	< 0.1
Tetraodontidae (unidentified)	3	6.7	33	0.8
Cephalopods	**45**	**100.0**	**1391**	**32.5**
Loliginidae	**8**	**17.8**	**20**	**0.5**
Loligo sp.	8	17.8	20	0.5
Lycoteuthidae	**6**	**13.3**	**11**	**0.3**
Lycoteuthis sp. 1	2	4.4	4	< 0.1
Lycoteuthis sp. 2	2	4.4	5	0.1
Selenoteuthis sp.	2	4.4	2	< 0.1
Enoploteuthidae	**37**	**82.2**	**1243**	**29.0**
Enoploteuthis chunii	30	66.7	1103	25.8
Abraliopsis lineata	20	44.4	140	3.3
Octopoteuthidae	**1**	**2.2**	**1**	**< 0.1**
Octopoteuthis sp. cf. *O. deletron*	1	2.2	1	< 0.1
Onychoteuthidae	**8**	**17.8**	**23**	**0.5**
Onychoteuthis banksii	8	17.8	23	0.5
Pholidoteuthidae	**2**	**4.4**	**2**	**< 0.1**
Pholidoteuthis sp. cf. *P. boschmai*	2	4.4	2	< 0.1
Histioteuthidae	3	6.7	4	< 0.1
Histioteuthis miranda	2	4.4	3	< 0.1
Histioteuthis sp.	1	2.2	1	< 0.1
Chtenopterygidae	**1**	**2.2**	**1**	**< 0.1**
Chtenopteryx sp. cf. *C. sicula*	1	2.2	1	< 0.1
Ommastrephidae	**28**	**62.2**	**80**	**1.9**
Sthenoteuthis oualaniensis	9	20.0	23	0.5
Eucleoteuthis luminosa	16	35.6	47	1.1
Ornithoteuthis volatilus	5	11.1	8	0.2
Ommastrephidae (unidentified)	2	4.4	2	< 0.1
Thysanoteuthidae	**1**	**2.2**	**1**	**< 0.1**
Thysanoteuthis rhombus	1	2.2	1	< 0.1
Mastigoteuthidae	**2**	**4.4**	**2**	**< 0.1**
Mastigoteuthis sp.	2	4.4	2	< 0.1
Cranchiidae	**2**	**4.4**	**2**	**< 0.1**
Galiteuthis sp. cf. *G. armata*	1	2.2	1	< 0.1
Galiteuthis sp. cf. *G. pacifica*	1	2.2	1	< 0.1
Tremoctopodidae	**1**	**2.2**	**1**	**< 0.1**
Tremoctopus violaceus	1	2.2	1	< 0.1

“Frequency of occurrence”, the number of stomachs in which that species was found; “Number”, the total number of times a species was recovered from all stomachs.

Ommastrephidae, found in more than 60% of the stomachs examined. The enoploteuthid squid, *Enoploteuthis chunii*, was the primary prey and represented 25.8% of the total, with an overall occurrence of 66.7%. The lanternfish, *Myctophum asperum*, ranked second and made up 20.3% of the total number of prey ingested, with an overall occurrence of 42.2%. Another lanternfish, *Diaphus schmidti*, was the third most abundant prey item representing 13.2% of the total, with an occurrence of 46.7% by number.

Twenty-eight of the prey species belonging to the lanternfish family Myctophidae made up 49.3% of the total prey and occurred in 82.2% of the stomachs examined. Two species of the family Enoploteuthidae were the dominant cephalopods ingested and represented 29.0% of the total with an overall frequency of occurrence of 82.2% of the stomachs (Table 1).

Table 2. Regression equation, and information used in estimating standard length and weight for the 13 major species in the diet of pantropical spotted dolphin from the eastern waters of Taiwan

Species	Regression equation	r^2	*n*	Reference
Fish				
Myctophum asperum	$y = 5.3621 + 18.8036\,x$	0.931	56	This study
Diaphus schmidti	$y = -17.1602 + 23.8106\,x$	0.940	13	This study
Diaphus watasei	$y = -15.4378 + 22.0426\,x$	0.952	9	This study
Engraulis japonicus	$\ln y = 3.4527 + 0.9812 \ln x$	0.939	168	Smale et al. 1995
Trichiurus lepturus	$y = 65.8751 + 120.5387\,x$	0.933	8	This study
Decaptuerus macrosoma	$y = - 42.451 + 47.561\,x$	0.934	12	This study
Scomber australasicus	$y = -275.3961 + 118.0851\,x$	0.977	6	This study
Scomber japonicus	$\ln y = 3.6437 + 1.2317 \ln x$	0.968	163	Smale et al. 1995
Lampanyctodes hectoris	$\ln y = 2.9403 + 1.3463 \ln x$	0.900	103	Smale et al. 1995
Cephalopods				
Enoploteuthis chunii	$y = 3.520 + 17.942\,x$	0.986	48	This study
Sthenoteuthis oualaniensis	$y = 6.98 + 39.25\,x$			Clarke 1986b
Euleoteuthis luminosa	$y = 11.12 + 37.61\,x$			Clarke 1986b
Onychoteuthis banksii	$y = -28.9 + 61.0\,x$			Clarke 1986b

"*x*", standard length or dorsal mantle length; "*y*", otolith length or lower rostral length.

Table 3. Information on the length-weight relationships [weight = a(length)^b] used to estimate the weight for the 13 major species in the diet of the pantropical spotted dolphin from the eastern waters of Taiwan

Species	Regression equation	r^2	*n*	Reference
Fish				
Myctophum asperum	$\ln w = -0.9400 + 2.2311 \ln x$	0.923	56	This study
Diaphus schmidti	$\ln w = -3.2705 + 3.7548 \ln x$	0.908	13	This study
Diaphus watasei	$\ln w = -2.6190 + 3.0922 \ln x$	0.931	9	This study
Engraulis japonicus	$\ln w = -1.0158 + 2.8541 \ln x$	0.937	168	Smale et al. 1995
Trichiurus lepturus	$\ln w = -0.0699 + 2.9280 \ln x$	0.920	8	This study
Decaptuerus macrosoma	$\ln w = -1.485 + 3.758 \ln x$	0.878	12	This study
Scomber australasicus	$\ln w = -2.9787 + 5.624 \ln x$	0.944	6	This study
Scomber japonicus	$\ln w = -0.7220 + 4.0055 \ln x$	0.958	163	Smale et al. 1995
Lampanyctodes hectoris	$\ln w = -2.5907 + 4.2197 \ln x$	0.878	97	Smale et al. 1995
Cephalopods				
Enoploteuthis chunii	$\ln w = -0.196 + 5.985 \ln x$	0.982	48	This study
Sthenoteuthis oualaniensis	$\ln w = 0.892 + 3.0 \ln x$			Clarke 1986b
Euleoteuthis luminosa	$\ln w = 0.718 + 2.75 \ln x$			Clarke 1986b
Onychoteuthis banksii	$\ln w = 0.58 + 3.70 \ln x$			Clarke 1986b

"*w*", the weight; "*x*", the otolith length or lower rostral length.

Estimation of prey size

Reliable regression equations were available for only 9 fish species and 4 cephalopod prey species identified in this study (Tables 2, 3). These 13 prey species made up 77.8% of the total number of prey consumed. The estimated length of the prey species ranged from 26.5 to 656.5 mm and the weight of the prey species ranged from 0.4 to 564.7 g (Table 4).

The most abundant fish prey species, *M. asperum*, ranged in size from 66.3 to 84.2 mm standard length with a mean length of 76.0 mm (SD, ± 3.7). The second abundant fish species, *Diaphus schmidti*, ranged from 26.5 to 53.0 mm standard length with a mean length of 42.0 mm (SD, ± 4.7). The reported maximum dorsal mantle length of *Enoploteuthis chunii* is 100 mm (Young et al. 1986). Estimated dorsal mantle lengths for this species in the stomach contents ranged from 61.0 to 82.0 mm with a mean length of 71.2 mm (SD, ± 6.5). Of the 13 species for which regressions were available, the longest prey ingested was the large-head hairtail, *Trichiurus lepturus*, which ranged from 496.2 to 656.6 mm standard length with a mean length of 555.0 mm and weight of 66.0 g. The largest prey species in terms of unit mass was the mackerel, *Scomber japonicus*, which had a mean standard length of 307.7 mm (SD, ± 19.8) and mean weight of 433.6 g (SD, ± 89.6).

Seasonal variation

A total, eighty-five taxa were identified in the stomach contents. The data matrices were standardized and analyzed by ANOSIM test, which demonstrated a significant difference ($R = 0.15$, $p < 0.01$) in similarities of samples between the 2 seasons, fall-winter and spring-summer. The SIMPER analysis identified 12 prey species that contributed to greater than 70% of the dissimilarity between the 2 seasons. These included 5 cephalopod species, *Enoploteuthis chunii*, *Sthenoteuthis oualaniensis*, *Eucleoteuthis luminosa*, *Abraliopsis lineata*, *Onychoteuthis banksii*, and 7 fish species, *Myctophum asperum*, *Diaphus watasei*, *Diaphus schmidti*, *Decapterus macrosoma*, an unidentified Tetraodontidae, *Engraulis japonicus*, and *Trichiurus lepturus* (Table 5). *Enoploteuthis chunii* ranked first and contributed 16.8% to the average dissimilarity. Comparing the average abundance by number between the 2 seasons, fall-winter and spring-summer, it is evident that the predominant prey species by number changed seasonally.

Table 4. Mean, standard deviation, and range of prey length (standard length in fish and dorsal mantle length in cephalopods) and weight of prey species consumed by the pantropical spotted dolphin, calculated with regression equations of otolith length or lower rostral length to prey length and weight

	Estimated prey length (mm)			Estimated weight (g)[a]			
Prey species	N	Mean ± SD	Range	Mean ± SD	Range	Total	%W
Fish							
Myctophum asperum	675	76.0 ± 3.7	66.3-84.2	7.51 ± 0.9	5.4-9.6	871	7.3%
Diaphus schmidti	396	42.0 ± 4.7	26.5-53.0	1.19 ± 0.3	0.4-2.2	564	0.8%
Diaphus watasei	167	126.4 ± 23.7	86.2-166.9	25.08 ± 12.5	8.2-50.1	203	5.7%
Engraulis japonicus	115	107.7 ± 8.8	93.0-128.4	12.92 ± 3.2	8.3-21.1	133	1.9%
Trichiurus lepturus	74	555.0 ± 40.3	496.2-656.5	66.04 ± 15.6	44.5-112.5	125	9.2%
Decaptuerus macrosoma	55	200.6 ± 13.9	161.1-222.0	105.5 ± 21.0	53.5-142.9	86	10.2%
Scomber australasicus	29	275.8 ± 49.0	163.9-332.7	317.6 ± 127.5	236.9-434.5	32	11.4%
Scomber japonicus	15	307.7 ± 19.8	280.0-335.0	433.6 ± 89.6	315.2-564.7	17	8.2%
Lampanyctodes hectoris	88	56.6 ± 5.5	44.3-67.1	2.4 ± 0.7	1.1-4.0	103	0.3%
Cephalopods							
Enoploteuthis chunii	877	71.2 ± 6.5	61.0-82.0	26.36 ± 6.43	15.9-38.0	1103	32.5%
Sthenoteuthis oualaniensis	23	210.3 ± 17.0	191.4-245.5	346.34 ± 92.61	253.3-548.4	23	8.9%
Euleoteuthis luminosa	47	113.7 ± 35.3	60.1-191.7	41.19 ± 36.46	4.2-153.2	47	2.2%
Onychoteuthis banksii	23	123.6 ± 15.3	93.1-143.1	55.4 ± 17.7	23.2-82.8	23	1.4%

[a]The percentage of the total contribution by weight for a given species is based only the total contribution by weight of these 13 species.

"N", the total number of fish otoliths or cephalopod beaks that were measurable, i.e., not broken or worn.

DISCUSSION

Our samples demonstrate that pantropical spotted dolphins eat a wide variety of fish and cephalopod prey. The 64 species of fish made up 67.5%, and 21 species of cephalopods made up 32.5% of the total number of prey ingested. Of these, mesopelagic prey were the primary species represented in the samples. Myctophid lanternfishes and enoploteuthid squid accounted for 78.3% of all prey consumed. Although regional faunal differences in prey species composition may be expected, our results are generally similar to the findings of Robertson and Chivers (1997) for this dolphin in the eastern tropical Pacific (ETP). In the ETP region, they also found that the percent by number of fish (66.6%) was higher than that for cephalopods (32.6%). There were also similarities in the prey consumed in that myctophid lanternfishes and species of the cephalopod families Enoploteuthidae and Ommastrephidae were dominant in their stomach samples.

Species of myctophid fish and enoploteuthid squid are most abundant in the mesopelagic zone. Squid of the family Enoploteuthidae demonstrate a number of characteristic features that may facilitate their being preyed upon by cetaceans, in that they typically have elaborate luminescent organs, are small in size, school in large numbers, and are diel vertical migrators (Clarke 1986b). The frequency of distribution of prey size collected or estimated from dolphin stomachs could shed light on the age structure of prey species consumed through this particular food chain, but also could reveal the foraging diurnal patterns. Many cephalopods are well known as diel vertical migrators. However, some variations in diel vertical migrating patterns have been demonstrated between adult and larval growth stages. Enoploteuthid larval squids are most abundant at depths of 100-150 m during the day, and at 30-50 m at night (Young et al. 1986). Adults occur at depths of 300-600 m during the day, migrating to the upper 150 m at night (Roper et al. 1975). Females of enoploteuthid squid are typically mature at about 50 mm dorsal mantle length (Kubota et al. 1982, Riddell 1982). Estimated dorsal mantle length for *E. chunii* in our stomach samples ranged from 61.0 to 82.0 mm which suggests that pantropical spotted dolphins off eastern Taiwan were feeding on adult *E. chunii*. The adult enoploteuthids migrated to shallower water layers in the evening, which caused them to be good candidates for food items. Our results indicated that our spotted dolphins may forage for squid at night at depths beyond upper 150 m. In the coastal waters of Taiwan, *E. chunii* has been previously reported from the stomach of 1 Cuvier's beaked whale beach stranded in northwestern Taiwan at Houlong, Miaoli County (Wang et al. 1995) Wang et al. (2003) also found that dwarf sperm whales and pygmy sperm whales primarily fed on *E. chunii*. These evidence shows that *E. chunii* may be an important food resource in Taiwanese waters.

Myctophid fishes are also very abundant in

Table 5. Average abundance of important prey species in groups W (fall-winter) and S (spring-summer) in the stomach contents of the pantropical spotted dolphin listed in order of their contribution to the average dissimilarity between the 2 groups, with a cut off when the cumulative percent contribution to average dissimilarity reaches 70%

Species	Average abundance of group W	Average abundance of group S	Average dissimilarity	Percent contribution	Cumulative percent contribution
Enoploteuthis chunii	34.6	10.7	15.1	17.0	17.0
Myctophum asperum	32.9	0.9	9.3	10.5	27.5
Diaphus watasei	0.4	10.1	7.6	8.6	36.1
Diaphus schmidti	17.6	5.6	6.7	7.6	43.6
Diaphus macrosoma	1.8	2.1	4.9	5.5	49.2
Abraliopsis lineata	2.6	3.8	4.7	5.3	54.5
Unidentified Tetraodontidae	0.5	1.1	3.1	3.5	58.0
Sthenoteuthis oualaniensis	0.2	0.9	2.4	2.7	60.6
Onychoteuthis banksii	0.2	1.0	2.3	2.6	63.3
Engraulis japonicus	5.1	0.1	2.2	2.5	65.7
Eucleoteuthis luminosa	1.2	0.8	2.0	2.3	68.0
Trichiurus lepturus	4.5	0.5	2.0	2.2	70.2

the mesopelagic zone, representing 25% of the biomass of all mesopelagic fishes (Karnella 1987, Tzeng 1989). Most myctophid species found in our study are known to undergo diel vertical migrations and are at depths of 200-700 m during the daytime and ascend to 0-200 m during the nighttime (Kawaguchi 1974). Myctophid fishes are also small in size and have elaborate photogenic light organs.

These mesopelagic prey species are associated with the deep scattering layer and most undergo diel vertical migrations, moving into the surface layer at dusk to feed and retreating to depths at dawn to avoid predation (Roper et al. 1975, Mccrone 1981, Karnella 1987, Sogard et al. 1987, Tzeng 1989, Chiu 1991). Pantropical spotted dolphin may primarily feed at night and may occur in layers shallower than 200 m as reported in another study (Baird et al. 2001).

In Hawaii *S. attenuata* is reported to feed primarily on diurnally migrating myctophid fish as well as enoploteuthid and ommastrephid cephalopods (Shomura et al. 1965, Clarke 1998). Recent studies using time-depth recorder-tagged *S. attenuata* in Hawaii have revealed a marked increase in dive activity after dark suggesting that spotted dolphins in this region feed primarily at night (Baird et al. 2001). Robertson and Chivers (1997) used the stomach fullness index (SFI) technique of Bernard and Hohn (1989) to analyze their spotted dolphin stomach samples from the ETP. In this region they found that the SFI was highest in the morning hours (0600-0900), suggesting that pantropical spotted dolphin fed during the night when their prey are nearest the surface.

The average abundance of some commercial fish found in the samples of dolphin stomachs from Taiwan correspond with the fisheries production by season (Fig. 1). According to the fish landing records of 1994-1995 in the Fisheries Yearbook in Taiwan (Anon. 1995 1996), the fisheries catch of spotted chub mackerel, *Scomber australasicus*; chub mackerel, *Scomber japonicus*; and largehead hairtail, *Trichiurus lepturus*; is higher during fall and winter (Oct.-Mar.), while fisheries catch of shortfin scad, *Decapterus macrosoma*, is higher during spring and summer. The Japanese anchovy, *Engraulis japonicus*, migrates into the eastern waters of Taiwan to spawn during Feb. and Mar. (Shen 1971, Young et al. 1992). The purpleback flying squid, *Sthenoteuthis oualaniensis*, is used for bait in the longline fisheries, it migrates into the eastern waters of Taiwan, and the fisheries catch reaches its peak during May through Aug. (Dong 1981). These species had higher average abundance by number in the stomach contents of this cetacean during the same fishing season. This consistent phenomenon supports the pantropical spotted dolphin being an opportunistic feeder.

This conclusion is also supported by other studies on various dolphin species (Brown et al. 1965, Jones 1981, Fiscus 1982, Gaskin 1982, Ross 1984, Evans 1987, Young et al. 1994, Robertson et al. 1997). Pantropical spotted dolphins were associated with the warmest water in the southeastern waters of Taiwan, and while they could be sighted year round (Yeh 2000), they were sighted more often in summer and fall in the northeastern waters of Taiwan (Chen 2001). Seasonal changes in prey composition could be a result of many factors such as prey seasonal movements or migration, prey spawning seasons, or simply prey distribution. It has been suggested that dolphin movements may correspond to the movement or availability, of prey (Jones 1981, Reilly 1990, Young et al. 1994, Robertson et al. 1997, Silva 1999). The stomach contents of opportunistic feeders in different geographic regions may not only reflect the fish and cephalopod fauna (Young et al. 1994), but may also shed light on their temporal fluctuations in an area. Hence, in addition to providing information on predator-prey relationships, dietary studies of cetaceans can also be used to monitor the distribution and seasonal variations of natural resources of dolphin prey species.

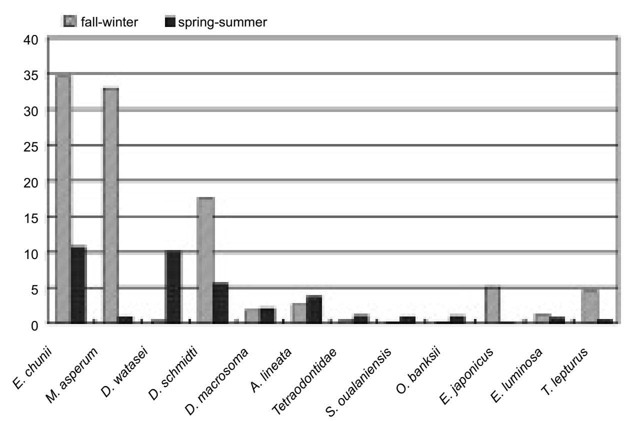

Fig. 1. Average abundance of important prey species in fall-winter and spring-summer in the stomach contents of the pantropical spotted dolphin.

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