FOOD AND FEEDING OF JUMBO SQUID *DOSIDICUS GIGAS* IN THE CENTRAL GULF OF CALIFORNIA DURING 2005–2007

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ABSTRACT

Stomach contents were analyzed for 249 jumbo squid (*Dosidicus gigas*) of 35–80 cm mantle length. All squid were sampled in the central Gulf of California in 2005–07, primarily on the commercial fishing grounds of Santa Rosalia during different times of the year. Diet off Santa Rosalia was mainly composed of mesopelagic micronektonic organisms, mostly the myctophids *Benthosema panamense*, *Triphoturus mexicanus*, and the squid *Pterygioteuthis giardi*. Pteropods and crustaceans made up a smaller portion of the diet. Squid sampled elsewhere revealed that the pelagic red crab, *Pleuroncodes planipes*, and northern anchovy, *Engraulis mordax*, could also be major dietary items. Cannibalism incidence increased with squid mantle length. We propose that the main prey of jumbo squid in the central Gulf of California derives from the mesopelagic community associated with the upper boundary of the oxygen minimum layer, a well-developed midwater feature in this region. In addition, opportunistic foraging on a variety of organisms supplements their dietary intake. These data are discussed in conjunction with recent electronic tagging data that revealed vertical and horizontal movements of jumbo squid. This work demonstrates a need to study the dynamics of the oxygen minimum layer and the composition of the deep-scattering layer over the upper slope of Guaymas basin.

INTRODUCTION

The first phase of commercial fishing for jumbo squid, *Dosidicus gigas*, in the Gulf of California began in 1974 and ended in 1981 (Ehrhardt et al. 1983). The fishery collapsed during and after the strong 1982–83 El Niño. Up to that time, stomach content analysis showed that jumbo squid from the Gulf fed mainly on neritic and small pelagic fishes (sardines, mackerels), pelagic red crab, and myctophids, with cannibalism also occurring (García-Domínguez and González-Ramírez 1988, Ehrhardt 1991). Ehrhardt (1991) therefore suggested that jumbo squid may have effects on the important commercial sar-

dine resource. This paper is arguably the most historically influential study of *Dosidicus* diet, and the conclusion of sardine predation has been widely cited in reviews on cephalopod feeding (see Boyle and Rodhouse, 2005).

A largely artisanal fishery resumed in 1994 for a form of *D. gigas* that matures at a large size (40–85 cm mantle length, ML), operating close to shore in the Guaymas Basin, both in the States of Sonora and Baja California Sur. Annual landings were over 100,000 tonnes in 1995–97. During this period most squid were taken off Santa Rosalia, Baja California, between May and November, and the remaining off Guaymas, Sonora, between December and April (Markaida and Sosa-Nishizaki 2001). In contrast to results of earlier studies, Markaida and Sosa-Nishizaki (2003) found that these large squid fed mostly on mesopelagic micronekton, mainly myctophids.

The squid fishery in the central Gulf collapsed again in 1998 following the 1997–98 El Niño. Smaller squid that matured at <45 cm ML re-established the fishery in the following year after a transition to La Niña conditions. These smaller squid again fed mostly on myctophids (Markaida 2006). Since 2000, large squid have again dominated the fishery in the central Gulf (Nevárez-Martínez et al. 2006; Bazzino et al. 2007), but dietary studies have not been reported during this period.

This paper presents an analysis of jumbo squid feeding in the central Gulf of California during the period of 2005–07 based on samples made on the commercial fishing grounds off Santa Rosalia during different times of the year and on samples opportunistically collected from elsewhere in the Gulf. Diet was mainly composed of mesopelagic micronekton, primarily myctophid fishes. Although opportunistic foraging on anchovies and other small fishes does occur, no evidence of sardine predation was found.

Recently (since 2002), *Dosidicus gigas* has undergone a major northern range expansion to as far north as southeast Alaska (Wing 2006). Because *Dosidicus gigas* is an abundant and highly migratory predator, shifts in diet
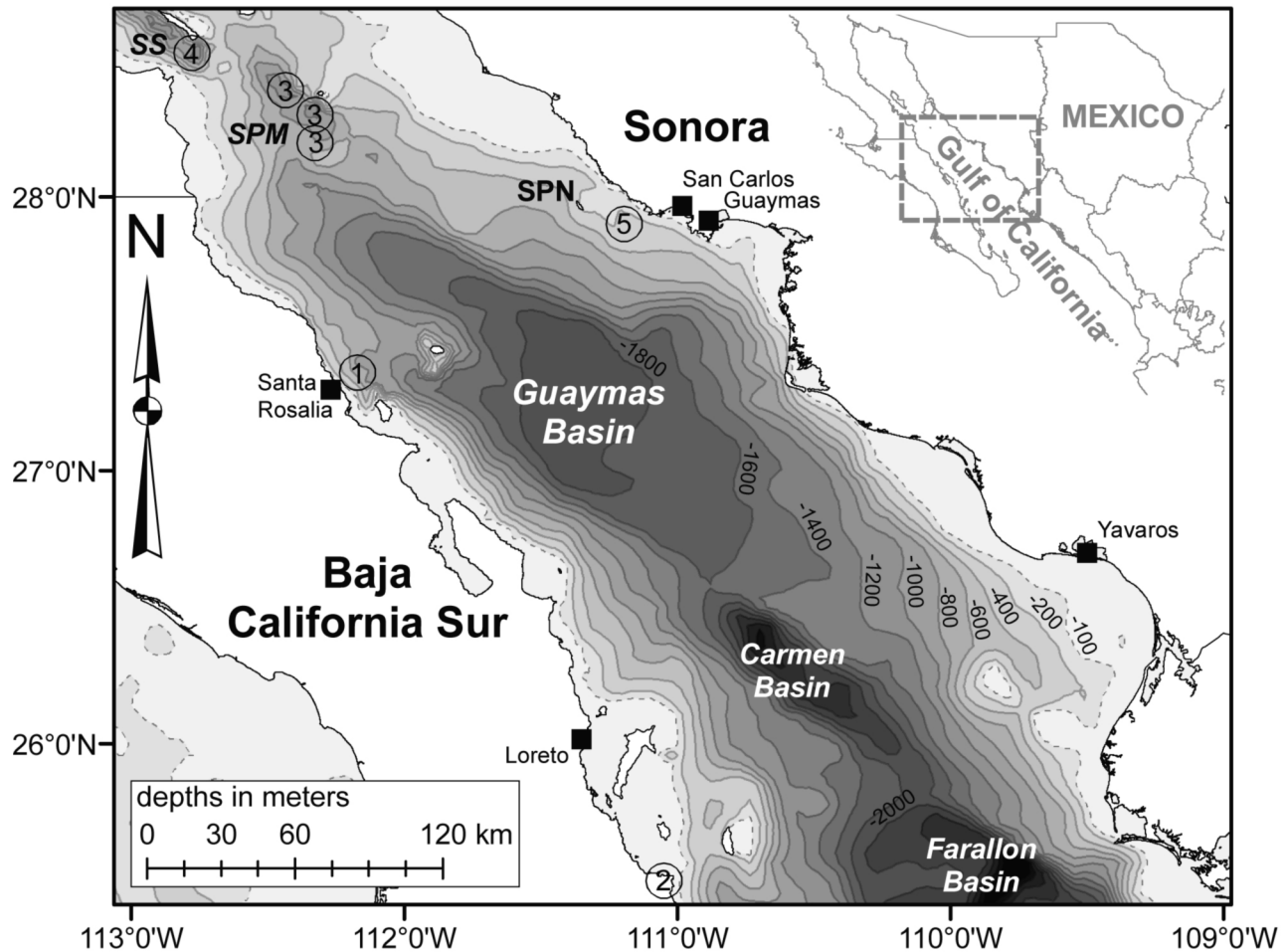
Figure 1.   Central Gulf of California showing locations (as listed in Table 1) where samples were taken by number and name as used in text: 1 - Santa Rosalia; 2 - Point San Marcial; 3 - San Pedro Martir Basin (SPM); 4 - Salsipuedes Basin (SS); and 5 - San Carlos. Basin names are in italics. SPN is San Pedro Nolasco Island. Depths are in meters.

likely have important ecological implications, including possible impacts to commercially important groundfish stocks. Thus, it is important to compare dietary content of squid in the core location of the central Gulf to that in newly invaded areas to the north. Stomach contents from squid sampled in the Pacific Ocean, both off the Baja peninsula in Mexico (Bazzino et al., submitted) and off northern California (Field et al. 2007), clearly show that *Dosidicus* forages not only on micronekton, but also on a variety of neritic resources, including hake and, in the California case, sardines. The goal of this study was to monitor dietary changes in association with temporal and spatial changes in abundance of this opportunistic predator.

MATERIALS AND METHODS

Jumbo squid were collected by jigging, generally after dusk, in the central Gulf of California during 2005–07 (see fig. 1). Stomachs of 249 squid from nine samples (a group of stomachs, collected at a given locality and date)

were analyzed. These included five samples collected on the Santa Rosalia fishing grounds at various times of the year between June 2005 and November 2007. Samples were also collected from the northern basins of San Pedro Martir and Salsipuedes in July 2006 and from San Carlos, Sonora, in March 2007. Another sample was obtained from animals discovered in the intertidal after a stranding at Point San Marcial, Baja California Sur, in May 2006. Sample size ranged from 10 to 57 stomachs (tab. 1). The dorsal ML (to the nearest mm) was measured in all squid except for the Point San Marcial sample (these squid were in the 25–30 cm ML range) and for 16 animals from San Pedro Martir basin. Sex and stage of maturity were assigned according to Lipiński and Underhill (1995). All squid analyzed in this study belong to the form of *Dosidicus gigas* that matures at large body size, with mature females ranging 40–82 cm ML and mature males 41–74 cm ML (see fig. 2).

Stomachs were kept frozen at −20°C until analysis in the laboratory. A subjective, visual stomach fullness index

TABLE 1
Summary data for jumbo squid (*Dosidicus gigas*) collected for stomach contents analysis
in the Gulf of California during 2005–07.

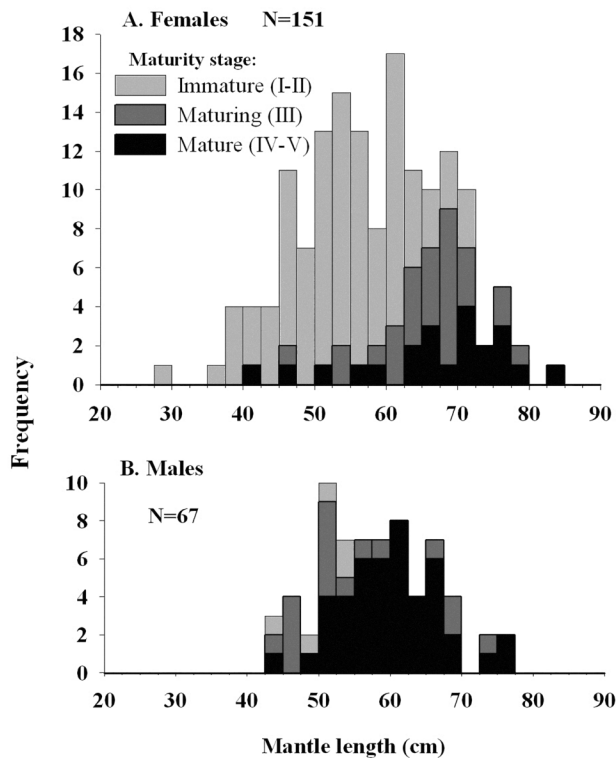| Location	Date	Sex			Total	MLᵃ (cm)
		Females	Males	Unknown		
Santa Rosalía	13 Jun 2005	16	13	1	30	41–67
	6–14 Jul 2006	19	7		26	49–72
	20 Oct 2006	11	3		14	66–82
	22 Mar 2007	22	15		37	41–74
	10 Nov 2007	19	14		33	46–73
Point San Marcialᵇ	17 May 2006			22	22	25–30
San Pedro Mártir	17, 20, 21 Jul 2006	35	6	16	57	25–81
Salsipuedes Basin	18 Jul 2006	14	4	2	20	44–73
San Carlos	13, 18 Mar 2007	9	1		10	38–70
Total		145	63	41	249	25–82

ᵃML, mantle length
ᵇStranded individuals

Figure 2.   Distribution of ML and sexual maturity state for female (A) and male (B) jumbo squid (*Dosidicus gigas*) collected in the central Gulf of California for stomach content analysis.

and complete separation of prey for weighing (Breiby and Jobling 1985). For this reason, only the most conspicuous prey items were weighed to the nearest 0.1 g.

Identification of fish sagittal otoliths was made by consulting available keys (Fitch and Brownell 1968; Fitch 1969a, b; Harvey et al. 2000; García-Godos Naveda 2001; Mascareñas-Osorio et al. 2003). Cephalopod beaks were identified following Clarke (1986). Reference collections held at Laboratorio de Pesquerías Artesanales at ECOSUR Unidad Campeche were also used to identify otoliths and squid beaks. Undigested pieces of squid flesh, indicative of cannibalism, were considered apart from other prey (see Markaida and Sosa–Nishizaki 2003). Pelagic gastropods were identified after McGowan (1968). Crustaceans were identified by their exoskeleton. The number of fish or cephalopods consumed was estimated as the maximum number of right or left fish otoliths, or of upper or lower cephalopod beaks (Antonelis et al. 1984). When prey lenses were more numerous than otoliths or beaks, they were counted as fish lens pairs or as the maximum number of proximal or distal sections of cephalopod lenses, divided by two.

Frequency of occurrence, numeric, and gravimetric (volumetric) methods were used to quantify diet. Frequency of occurrence (%FO) was calculated as the percentage of stomachs in which the prey occurs in any given sample. Number (%N) is the percentage of stomachs in which the prey occurs relative to the total number of stomachs, and weight (%W) is defined as the wet weight of a certain prey type relative to the total wet weight of all prey. %N and %W were calculated from data pooled from all stomach contents in a given sample and expressed as percentages (Cailliet 1977). Graphs of the index of relative importance, IRI = (%N + %W) × (%FO) were plotted to illustrate monthly diet composition following Pinkas et al. (1971). Only prey species or taxa with IRI values >1% were included in this analysis.

(FI) was assigned: 0, empty; 1, scarce remains; 2, half full; 3, almost full; and 4, completely full (Breiby and Jobling 1985). In order to preserve hard remains of prey for identification, stomach contents were screened through a 0.5 mm mesh sieve with gentle washing. The screened contents were observed under a binocular dissection microscope (60–120×) over both a black and a white background to aid recognition. The advanced degree of digestion of stomach contents generally impedes exact
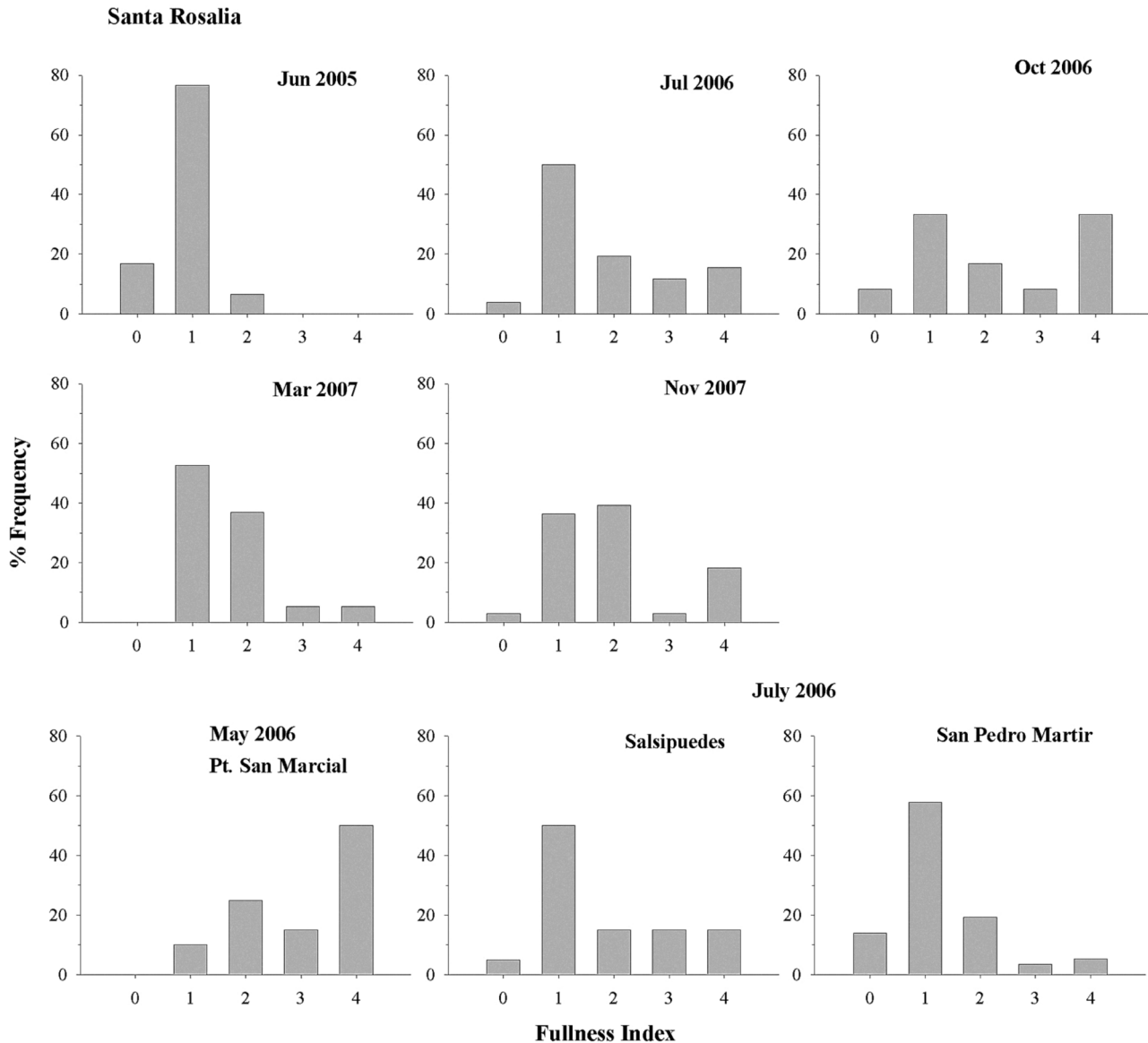
Figure 3. Frequency of occurrence for the range of stomach fullness indices across localities and seasons in the central Gulf of California during 2005–07.

The lengths of up to 15 of the best preserved otoliths of each fish species per stomach were measured to the nearest 0.1 mm. The size of ingested fish was calculated from the otoliths using relationships for each species or genus (Aurioles-Gamboa 1991; Harvey et al. 2000; Markaida and Sosa-Nishizaki 2003). The relationships between total length (TL, mm), standard length (SL, mm), body weight (BW, g), and otolith length (OL, mm) for a sample of *Triphoturus mexicanus* we collected in the central Gulf were calculated as follows:

$$TL = 15.0324 + 39.4418 \text{ OL} \quad r^2 = 0.71 \quad n = 81$$

$$SL = 14.0445 + 28.5722 \text{ OL} \quad r^2 = 0.60 \quad n = 101$$

$$BW = 0.6437 \times OL^{2.1481} \quad r^2 = 0.53 \quad n = 101$$

Lower rostral lengths (LRL) of squid beaks were measured to the nearest 0.1 mm. Upper beak dimensions were used in the absence of lower beaks. Ingested squid ML and BW were estimated using the relationships provided by Clarke (1986) and Wolff (1984). Relative prey size was calculated as the percentage of estimated prey size (TL or ML) relative to jumbo squid ML. Correlation between relative prey size and squid size was tested for the most numerous prey species.

RESULTS

Stomach Fullness

The stomach fullness index was observed for 218 squid (fig. 3). They were not recorded for 27 stomachs taken

TABLE 2
**Frequency of occurrence (FO), number, and weight of prey in the stomach contents of
249 jumbo squid (*Dosidicus gigas*) from the Gulf of California during 2005–07.**

Prey	FO	FO%	N	N%	g	W%
	FO		**Number**		**Weight**	
PISCES	129	51.8	530	44.0	271.9	9.5
Myctophidae:	77	30.9	380	31.5	87.2	3.0
Benthosema panamense	56	22.5	206	17.1	74.6	2.6
Triphoturus mexicanus	23	9.2	153	12.7	0.0	0.0
Diogenichthys laternatus	9	3.6	11	0.9	0.0	0.0
Unidentified Myctophidae	10	4.0	10	0.8	12.6	0.4
Photichthydae:						
Vinciguerria lucetia	6	2.4	8	0.7		
Engraulidae:						
Engraulis mordax	32	12.9	86	7.1	109.0	3.8
Merlucciidae						
Merluccius angustimanus	3	1.2	3	0.2		
Batrachoididae:						
Porichthys sp.	2	0.8	2	0.2		
Carangidae:						
Trachurus symmetricus	1	0.4	1	0.1	3.2	0.1
Scombridae:						
Scomber japonicus	3	1.2	3	0.2	9.4	0.3
Argentinidae:						
Argentina sialis	1	0.4	1	0.1		
Unidentified Teleostei	30	12.0	46	3.8	63.1	2.2
CEPHALOPODA	79	31.7	459	38.1	5.4	0.2
Pyroteuthidae:						
Pterygioteuthis giardi	55	22.1	333	27.6	2.1	0.1
Gonatidae:						
Gonatus sp.	10	4.0	11	0.9		
Enoploteuthidae:						
Abraliopsis affinis	7	2.8	10	0.8		
Octopoda:						
Octopus sp.	1	0.4	1	0.1		
Unidentified Cephalopoda	26	10.4	104	8.6	3.3	0.1
PTEROPODA						
Unidentified Thecosomata	14	5.6	71	5.9		
CRUSTACEA	20	8.0	44	3.7	136.0	4.7
Euphausiacea	1	0.4	1	0.1		
Isopoda	1	0.4	1	0.1		
Copepoda	1	0.4	6	0.5		
Unidentified Decapoda	1	0.4	1	0.1	22.4	0.8
Pleuroncodes planipes	14	5.6	32	2.7	113.6	4.0
Brachiura	3	1.2	3	0.2		
Unidentified Crustacea	12	4.8	17	1.4	6.9	0.2
Algae, sediments	9	3.6	9	9	19.9	0.7
Unidentified organic matter	58	23.3			487.1	17.0
Cannibalism	74	29.7	75	6.2	1943.6	67.7
TOTAL	1205	100	249		2870.66	

in March 2007 and for a total of four stomachs from other samples. Overall, 8.2% were empty, 49% had little trace of food, 22% were half full, 6.4% were almost full, and 14.2% were completely full. Most stomach samples from Santa Rosalia were no more than half full. The relatively large number of full stomachs in October 2006 and November 2007 was due to cannibalism. Stomach fullness index distributions did not significantly differ between three samples taken in July 2006 (Santa Rosalia, San Pedro Martir, and Salsipuedes basins), with most stomachs ($\geq$50%) containing little food (Chi-square test, $\chi^2 = 7.02$, d.f. = 8, $p > 0.05$). The sample of squid
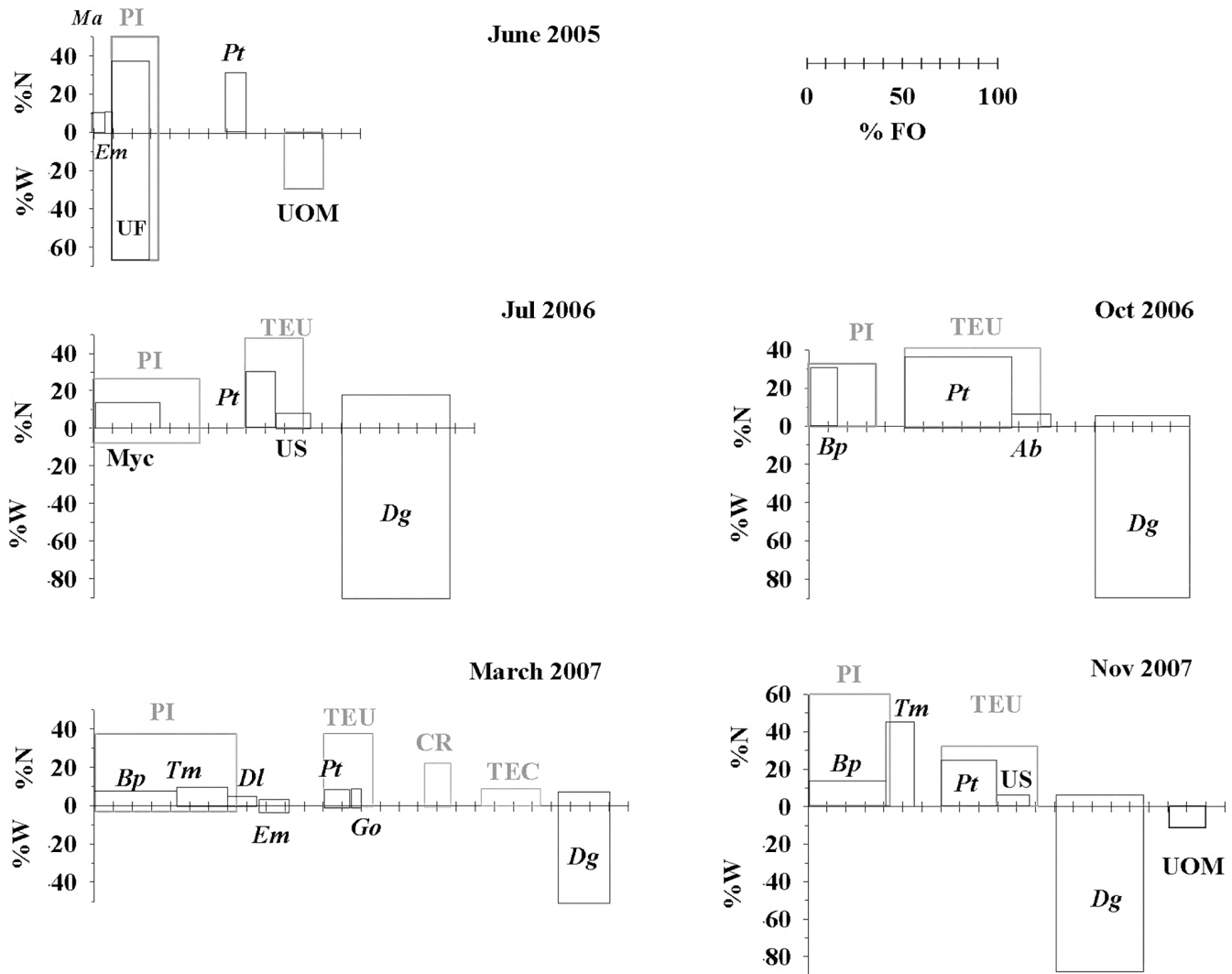
Figure 4.   Monthly composition by percentage number (%N) and weight (%W) (vertical axis) and frequency of occurrence (%FO, horizontal axis) of prey found in the stomach contents of jumbo squid (*Dosidicus gigas*) collected off Santa Rosalia, 2005–2007. Myc, Myctophidae; *Bp, Benthosema panamense*; *Tm, Triphoturus mexicanus*; *Dl, Diogenychthys laternatus*; *Ma, Merluccius angustimanus*; *Em, Engraulis mordax*; UF, Unidentified fish; *Pt, Pterygioteuthis giardi*; *Ab, Abraliopsis affinis*; *Go, Gonatus* spp.; US, Unidentified squid; *Dg, Dosidicus gigas*; and UOM, Unidentified organic matter. Large prey groups in grey: PI, Pisces; TEU, Teuthoidea; TEC, Thecosomata; and CR, Crustacea. The illustrated %FO scale applies to all panels (1 small division = 10%).

stranded at Pt. San Marcial was unusual in that half of the stomachs were completely full (fig. 3).

Diet Description

Stomach contents of jumbo squid revealed three main groups of prey: fishes, molluscs (cephalopods and pteropods), and crustaceans (tab. 2). Fishes occurred in over half of the stomachs and accounted for 44 %N. Myctophids were the most abundant and frequent fish and accounted for 31% of all prey, both by number and occurrence. *Benthosema panamense* was the dominant myctophid, accounting for 22 %FO and 17 %N. Another myctophid, *Triphoturus mexicanus*, accounted for 9.2 %FO

and 12.7 %N. Similar to the case of myctophids, unidentified teleosts had a 30 %FO and formed a fairly consistent component of the diet in most of the samples (see next section). Although the anchovy, *Engraulis mordax*, has a large %FO in Table 2, it was a significant prey item in only two samples (see below).

Cephalopods were next in importance; they were found in 32% of stomachs, and accounted for 38% of all prey by number. Micronektonic squid, *Pterygioteuthis giardi*, dominated, accounting for 22 %FO and 27 %N. Unidentified cephalopods, represented by lenses with 10 %FO and 8.6 %N, probably belong to *P. giardi* as well. Pteropods and crustaceans were relatively minor com-
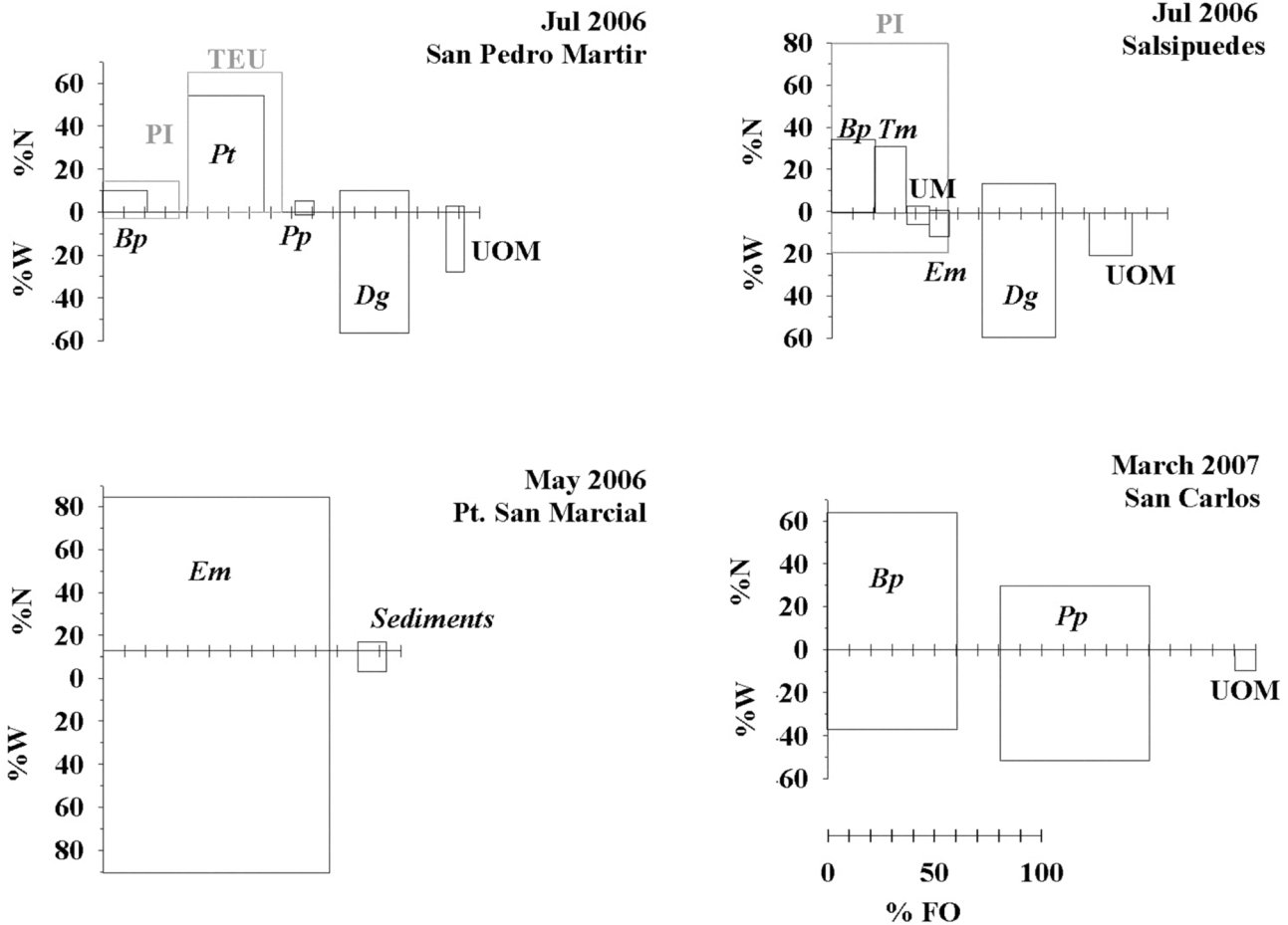
Figure 5. Composition by percentage number (%N) and weight (%W)(vertical axis) and frequency of occurrence (%FO, horizontal axis) of prey found in the stomach contents of jumbo squid (*Dosidicus gigas*) collected in several localities of the central Gulf of California, 2005–07. *Bp, Benthosema panamense*; *Tm, Triphoturus mexicanus*; UM, Unidentified myctophid; *Em, Engraulis mordax*; *Pt, Pterygioteuthis giardi*; *Pp, Pleuroncodes planipes*; *Dg, Dosidicus gigas*; and UOM, Unidentified organic matter. Large prey groups in grey, as in Figure 4.

ponents of stomach contents overall, but the pelagic red crab, *Pleuroncodes planipes*, was a dominant prey species in one sample (see below). Most of the weight of the stomach contents consisted of cannibalized squid (68%) and unidentified organic matter (17%).

Temporal Variation

Temporal variation in jumbo squid diet was assessed over the course of non-consecutive months at Santa Rosalia (fig. 4). The stomach contents of squid taken in June 2005 were dominated by unidentified fish (36 %N and 67 %W), and to a lesser degree by the squid *P. giardi* (31 %FO). In every other sample from this area, an assortment of micronektonic mesopelagic prey dominated the diet. The squid *P. giardi* and other small squids were reasonably abundant, along with myctophids (mostly *B. panamense* and *T. mexicanus*). Myctophids dominated in March 2007 (81 %FO), whereas *P. giardi* was more frequent and abundant in October 2006 (57 %FO and 40 %N). In July 2006 myctophids occurred in 38% of

stomachs while *P. giardi* accounted for 33% of all prey by number. In November 2007, *B. panamense* occurred in 39% of stomachs, *T. mexicanus* accounted for 43% of all prey, and *P. giardi* were 39 %FO and 25 %N. While the relative importance of fishes (PI) and squids (TEU) varies, a strong seasonality in diet in the Santa Rosalia area was not evident over this time period (fig. 4), although the abundance of unidentified fish in June 2005 may reflect some seasonal change.

Regional Variation

Diet varied to a much greater degree between different sampling sites than between different time points in Santa Rosalia (fig. 5). A sample from the San Pedro Martir Basin (July 2006) was dominated by micronektonic squid, *P. giardi* (35 %FO and 56 %N), and the myctophid, *B. panamense*. Stomach contents of squid caught in the nearby Salsipuedes Basin at the same time were dominated by fish, myctophids *B. panamense* and *T. mexicanus*, but were totally lacking in the squid, *P. giardi*. In
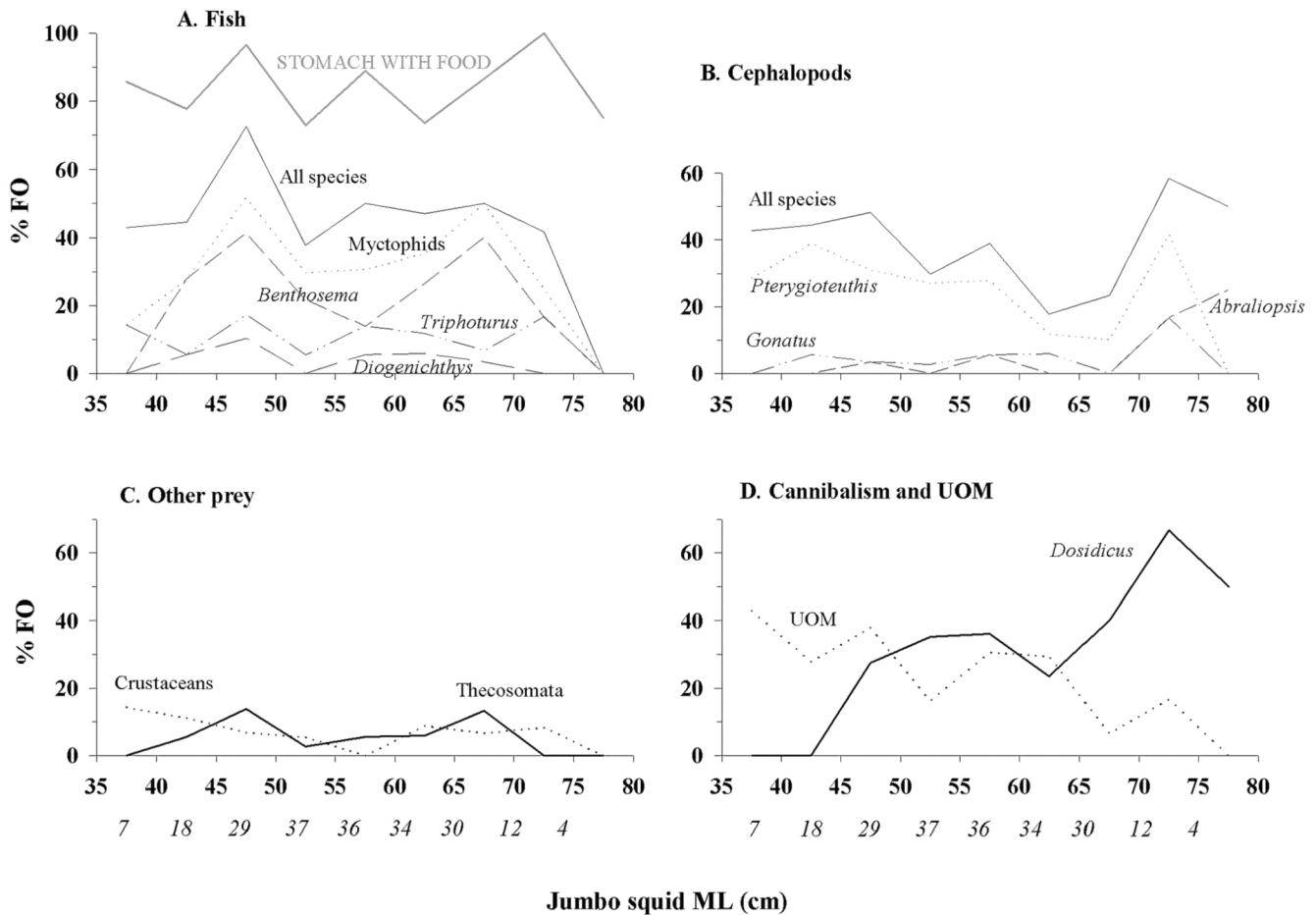
Figure 6. Frequency of occurrence of the most important prey of 207 jumbo squid (*Dosidicus gigas*) from the central Gulf of California during 2005–07 as a function of mantle size: (A) fish, (B) cephalopods, (C) crustaceans and Thecosomata, and (D) cannibalism and unidentified organic matter. Number of squid analyzed per size interval is given in italics at the bottom. Note that the fraction of non-empty stomachs is also plotted in panel A.

both samples, cannibalism accounted for most of the weight. The San Pedro Martir sample is thus quite similar to that collected in Santa Rosalia at the same time, whereas the Salsipuedes sample lacked micronektonic teuthoids.

Squid from San Carlos in March 2007 contained mostly *B. panamense* (60 %FO and 63 %N) and *P. planipes* (70 %FO, 29 %N, and half total weight). Stomachs of squid stranded at Point San Marcial contained only northern anchovy (%FO, %N, and %W ranged from 85–95%) (fig. 5). Both of these samples were qualitatively different from the ones discussed in the paragraph above.

Prey Type Versus Squid Size

Prey occurrence (%FO) versus squid size (35–82 cm ML, at 5 cm ML intervals) for 207 stomachs from the central Gulf of California is shown in Figure 6. Low values of %FO for the largest size interval (>75 cm ML) are skewed by the small number of very large animals. The frequency of empty stomachs varied between 4% and 27% with no clear dependence on ML (comple-

ment of "Stomachs with food" in fig. 6). Fishes, mainly myctophids, had moderately high occurrences (37–72%) in jumbo squid of all sizes (fig. 6A). Similarly, consumption of mesopelagic cephalopods, mostly *P. giardi*, is also quite high over the entire size range of squid (17–58%) (fig. 6B). Crustacean and pteropod (Thecosomata) occurrences were relatively low for squid of all sizes (fig. 6C). Although there was no clear dependence of any of these prey items on the size of the squid, cannibalism clearly increased with squid size. One in four squid in the 45–50 cm ML range showed evidence of cannibalism, whereas most squid >70 cm ML were cannibals. Occurrence of unidentified organic matter continuously decreased with squid size, from 42.8 %FO at 35–40 cm ML to 16.6 %FO at 70–75 cm ML (fig. 6D).

Prey Number

Major fish and cephalopod prey types were mainly represented by single occurrences, with numbers ranging from 1 to 10 (fig. 7). But the maximum number for some prey types including *P. giardi* (fig. 7D) was much
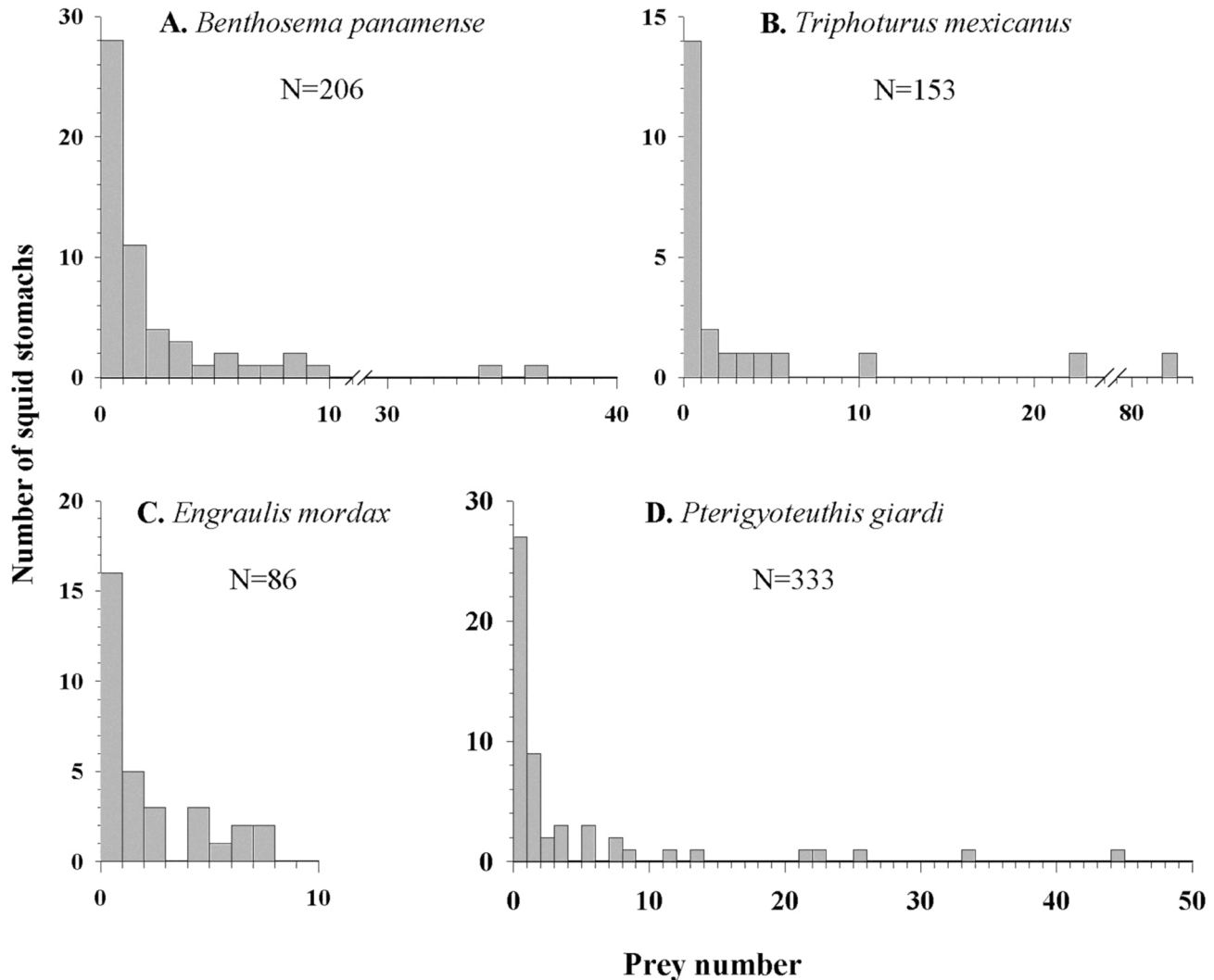
Figure 7. Frequency distributions of the number of prey items found in individual jumbo squid (*Dosidicus gigas*) stomachs from either counts of otoliths pairs for fishes: (A) *Benthosema panamense*; (B) *Thiphoturus mexicanus*; (C) *Engraulis mordax*; or beaks for squid (D) *Pterygioteuthis giardi*. The total number of prey items of each type are indicated on each panel.

larger, ranging from 36 (*B. panamense*, fig. 7A) to 83 (*T. mexicanus*, fig. 7B). Northern anchovy were the exception with a maximum number of eight found (fig. 7C); However, these squid were all quite small, and their stomachs were very full. With the exception of *P. planipes* and thecosomate pteropods (not illustrated), no more than two individuals of any other species were found in any one stomach.

Prey Size Versus Squid Size

Micronektonic myctophids (*B. panamense* and *T. mexicanus*) constituting the main prey of *D. gigas* were 33–66 mm in length, equivalent to 5–20% of jumbo squid ML. Micronektonic squid ranged from 13–37 mm ML, or 2–7% of jumbo squid ML. Weight of myctophids ranged from 0.2–1.5 g, and most squid weighed 0.1–1.8 g. Neritic prey such as northern anchovy ranged from

35–80 mm, equal to 8–30% of squid ML. The largest prey items found in this study were two Panama hakes (*Merluccius angustimanus*) 23 cm in standard length, about half the size of the ML of the squid that consumed them. Weight of these fish were more than 100-fold greater than that of typical micronektonic prey. Cannibalized squid were 16–36 cm ML and 37–64% of the consuming squid's ML (tab. 3). Figures 8A-C illustrate that prey sizes did not show any obvious dependence on the size of the consuming squid.

DISCUSSION

General Features of Diet

Jumbo squid collected by jigging in the central Gulf of California had some generally consistent features in their diet across all sample areas. They tended to forage

TABLE 3
Size of hard remains and estimated dimensions for prey of jumbo squid (*Dosidicus gigas*)
from the Gulf of California during 2005–07.

Prey	Number	Otolith length, mm			Standard length, mm			% Jumbo squid ML			Weight, g
		Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Range
Fish											
B. panamense	129	2.02	0.21	1.4–2.6	47.4[a]	5.3	32.6–61.7	8.4	1.8	5.6–20.1	0.27–1.5
T. mexicanus	84	0.95	0.13	0.7–1.3	52.5[a]	5.2	42.6–66.3	9.9	1.3	7.2–13.2	0.17–1.1
D. laternatus	6	1.03	0.05	1–1.1							
V. lucetia	6	1.66	0.22	1.4–1.9							
E. mordax	46	2.01	0.53	1.5–3.5	46.8	12.2	35.0–80.6	15.1	5.0	8.2–29.3	7.9–168
M. angustimanus	2	14.9		12.8–17	262		227–229	52.4		52.2–52.6	123–267
Argentina sialis	1	1									

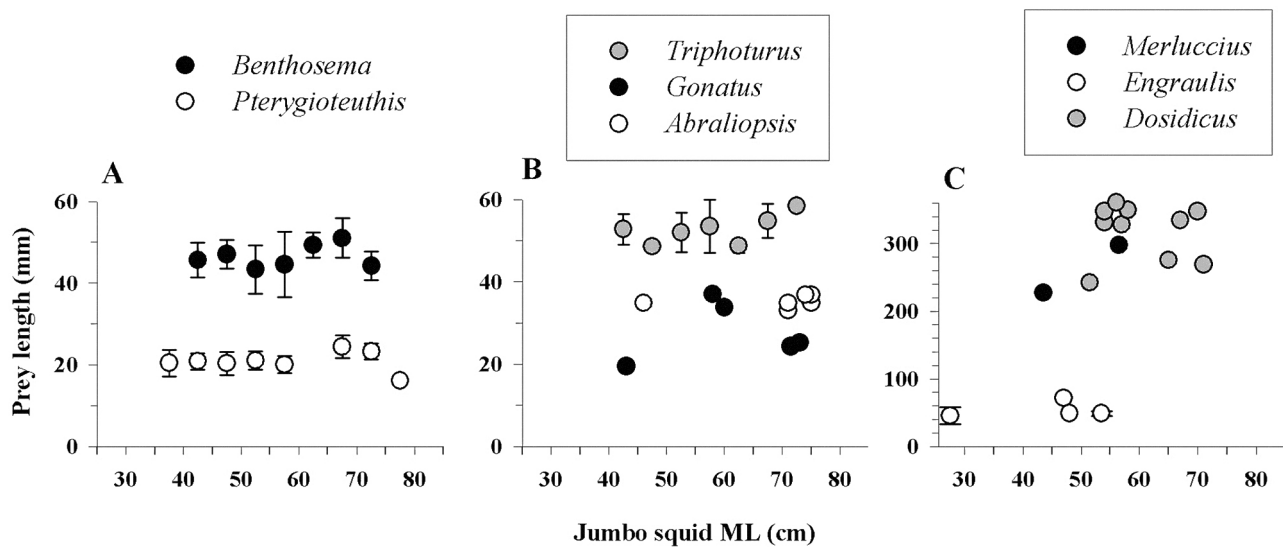|		Lower rostral length, mm			Mantle length, mm						
		Mean	S.D.	Range	Mean	S.D.	Range				
Squid											
P. giardi	172	0.44	0.07	0.2–0.6	20.9	2.6	13–27.7	3.9	0.7	2.1–7.2	0.07–1.6
Gonatus sp.	3	0.70	0.37	0.3–1.1	27.9	7.2	37–19.4	4.6	1.3	3.4–6.3	0.11–1.8
A. affinis	7	1.30	0.08	1.2–1.4	34.8	1.5	33–36.8	5.1	1.0	4.6–7.5	2.80–3.9
Cannibalism	14	5.81	1.76	1.6–7.4	295	66	166–360	54.1	9.1	37–64	9–995

[a]Total length, mm.

Figure 8. Body length of the most abundant prey found in jumbo squid (*Dosidicus gigas*) as a function of squid ML: (A) *Benthosema panamense* and *Pterygioteuthis giardi*; (B) *Triphoturus mexicanus*, *Gonatus* sp., and *Abraliopsis affinis*; and (C) *Merluccius angustimanus*, *Engraulis mordax,* and *Dosidicus gigas*. Total length is used for myctophids, ML for squid, and standard length for hake and northern anchovy.

primarily on an assortment of mesopelagic micronekton, specifically the myctophid fishes *Benthosema panamense* and *Triphoturus mexicanus*, and the squid *Pterygioteuthis giardi*. These primary prey species were characteristic of all sampling sites within the Guaymas Basin and San Pedro Martir Basin, with the exception of San Carlos, Sonora, where *Pleuroncodes planipes* was also a major prey item. Overall composition of prey species, frequency of occurrence of individual prey species, and size of prey items showed no dependence on squid ML between 40–70 cm, a range that largely makes up the commercial fishery. These results are in general agreement with previous data from the Gulf of California (Markaida and Sosa-Nishizaki 2003; Markaida 2006).

Myctophids are extremely abundant in the central Gulf of California and show a diel vertical migration to near-surface waters at night from daytime depths that are related to the upper boundary of the oxygen minimum layer (OML) (Robison 1972). This hypoxic mesopelagic environment is characteristic of the central

and southern Gulf of California at depths >250 m (Roden 1964; Álvarez-Borrego and Lara-Lara 1991). *T. mexicanus* is commonly associated with acoustic deep-scattering layers (DSL) at 300–400 m depth during daylight in this region (Dunlap 1970; Robison 1972), and this is likely to be the case for other major mesopelagic species comprising the diet of jumbo squid, particularly *B. panamense* and *P. giardi*. DSL communities were well developed during daytime over the upper slope of the Guaymas Basin off Santa Rosalia during our study (unpublished observations), and most of the prey consumed by jumbo squid in this region may thus constitute part of a mesopelagic boundary community (Reid et al. 1991). Recent electronic tagging studies of *Dosidicus gigas* in the Guaymas Basin show that the squid's vertical migrations are consistent with foraging on these species during both day and night (Gilly et al. 2006). Both squid and the DSL community spend daytime at depths associated with the OML and spend much of the night in near-surface waters.

Biases in Stomach Contents Analysis

Several biases may occur when analyzing stomach contents of squid taken by jigging. Cannibalism may be the largest concern, because *Dosidicus gigas* flesh was the most important dietary component by weight. These chunks of squid flesh were always fresh, indicating recent ingestion, and such cannibalistic attacks are commonly observed on impaired squid that are caught by the jig. Such behavior provoked by fishing is clearly unnatural and has been previously discussed (Markaida and Sosa-Nishizaki 2003). It remains unclear to what extent such attacks are launched on other squid in the absence of fishing efforts.

Additionally, hungry squid may be more likely to attack a jig, and this factor could be related to the relatively small number of prey remains often found in individual stomachs. However, squid with full stomachs are also caught by jigs (this paper and Bazzino et al., submitted).

Finally, some species of squid are known to discard the heads from larger fish prey (Collins and Pierce 1996), and identifying these fish by otoliths in the squid stomach would obviously not be possible. There is no evidence that *Dosidicus gigas* discard the heads of the small fishes that have been identified, but some predation on flesh of larger fishes cannot be ruled out.

Diet Variability on the Santa Rosalia Fishing Grounds

Santa Rosalia is the focus of the jumbo squid fishery on the Baja California coast, and this fishery generally runs from April or May until mid- to late-November. Sampling at Santa Rosalia during 2006–07 (March, July, October, and November) in the present study thus cov-

ers the entire traditional fishing season, although coverage is incomplete and not from a single season. All samples revealed the assortment of mesopelagic micronekton discussed in the previous section plus a significant amount of other fishes, mostly neritic and pelagic species, although no individual species was ever very abundant. The relative ranking of fish (PI in fig. 4) and squid (TEU) varied between samples, but both were always important by %N and %FO. Thus, there seems to be no marked seasonal variation in the diet of jumbo squid in the Santa Rosalia area, although a more complete sampling throughout the entire fishing season is still lacking.

The only sample from Santa Rosalia that did not fit with this picture was the one from June 2005. This sample was dominated by anchovy and unidentified fishes but still contained some of the standard micronekton seen in every other sample. As discussed below, we propose that this anomaly represents opportunistic feeding and demonstrates the need for systematic sampling to accurately characterize the diet of *Dosidicus gigas*.

Diet in Other Regions of the Central Gulf

More limited sampling in other parts of the Gulf does not allow detailed comparisons to the data from Santa Rosalia, but nonetheless some general points can be made. Two samples from July 2006 collected in the San Pedro Martir Basin and the nearby Salsipuedes Basin also displayed a diet of mixed micronekton similar to that observed in Santa Rosalia. The San Pedro Martir Basin is a northern extension of the Guaymas Basin, and samples from here were most similar. The Salsipuedes sample was also dominated by myctophids and other fishes, but lacked mesopelagic squids.

The latter comparison is particularly interesting. Despite the proximity of the San Pedro Martir and Salsipuedes sampling sites (fig. 1), the midwater physical environments of these areas are quite different because they are separated by a shallow sill (<200 m deep) that prevents mixing. As a result, the San Pedro Martir Basin has a well-developed OML (as do all the basins to the south), whereas the Salsipuedes Basin does not, due to strong tidal mixing and upwelling in the Ballenas Channel (Roden 1964; Álvarez-Borrego and Lara-Lara 1991). Oxygen concentration at the Salsipuedes site was >60 μM at depths of 500 m, compared to concentrations of <20 μM at 400 m depth at the San Pedro Martir sites (W. F. Gilly, unpublished data). Thus, jumbo squid do not appear to require the environment of the OML, at least on a time scale of days (migrations between the sites are possible). *B. panamense* is the most common mesopelagic fish north of the sill but *T. mexicanus* is also present (Robison 1972).

Two other samples are in marked contrast to the above generalization. Another micronektonic prey, *P. planipes*

(pelagic red crab), dominated stomach contents of squid in March 2007 off San Carlos, Sonora. At that time we observed dense schools of *P. planipes* at the surface over depths of 70–215 m between San Pedro Nolasco Island and San Carlos (unpublished observations). Although *P. planipes* is not commonly encountered in most of the central Gulf, large benthic abundances can occur on the upper shelf (at OML depths) along the area between San Pedro Martir Island and San Carlos/Guaymas in spring months (Arvizu-Martinez et al. 1974; Mathews et al. 1974).

P. planipes was previously found in jumbo squid diet during spring 1996 off Guaymas (Markaida and Sosa-Nishizaki 2003), and our observations in March 2007 are consistent with this pattern. Where and when they are available, *P. planipes* is clearly an important supplementary prey species for jumbo squid in the central Gulf. *P. planipes* is much more abundant in the Pacific Ocean, particularly off the southwestern coast of the Baja California peninsula (Boyd 1967), where it is the major prey for many pelagic predators, including jumbo squid (Sato 1974; Markaida 2006; Bazzino et al., submitted).

A second major deviation from the mixed micronekton diet occurred in the sample from Point San Marcial in May 2006. All of these rather small, immature squid had only anchovies in their stomach contents and most stomachs were completely full. Causes for such strandings are unknown (Gilly 2005), but clearly these squid had recently engaged in a mass foraging episode on anchovies. It is unknown how natural this type of feeding behavior is. For whatever reason, these squid had moved inshore to shallow waters from their normal deep habitat. What fraction of this group of squid was actually involved in the stranding is not clear. The comparatively low abundance of anchovy remains in other analyzed stomachs suggests that such feeding is unusual, but it does fit with the idea that *Dosidicus gigas* can be opportunistic.

Diet Stability Versus Opportunism

The diet of jumbo squid in the central Gulf of California, as exemplified by that observed in Santa Rosalia, is clearly dominated by mesopelagic micronekton, primarily myctophids and small squids that constitute mesopelagic boundary communities on the slopes of the Guaymas Basin as well as more northern basins such as San Pedro Martir. This mesopelagic assemblage typically resides in the upper boundary of the OML during the daytime and migrates to near-surface waters at night. It provides a reliable source of assorted micronekton, and hypoxia-tolerant jumbo squid probably continuously forage on these organisms over their entire vertical range (Gilly et al. 2006).

During the course of a traditional fishing season in Santa Rosalia (April/May to November) this pattern ap-

pears to be relatively stable, and diet does not vary appreciably during this period. Most squid are thought to leave the Santa Rosalia area by December and move to the winter fishing grounds off Guaymas (Markaida et al. 2005) or to other regions of the Gulf, possibly including San Pedro Martir (Gilly et al. 2006). At present, the connection between this seasonal exodus of jumbo squid from the Santa Rosalia area and the availability of the relevant local micronekton is unknown, but changes in the mesopelagic communities (Markaida 2006) or environmental factors (Markaida and Sosa-Nishizaki 2001) could be involved. Seasonal shifts in upwelling-driven primary productivity occur in this region as well, with productivity falling in winter along the Baja coast and rising along the Sonora coast (Roden 1964; Álvarez-Borrego and Lara-Lara 1991).

In contrast with this general pattern of stable foraging, *D. gigas* also shows a highly opportunistic mode of feeding that demonstrates great plasticity. In the present study this is most dramatically demonstrated by the selective feeding on anchovies that might cause them to strand at Point San Marcial (May 2006). Similarly, jumbo squid in the San Carlos/Guaymas area significantly supplement their diet of mesopelagic fare with *P. planipes*, an abundant but ephemeral springtime prey species. To a lesser extent, opportunistic foraging undoubtedly is responsible for consumption of the larger neritic and pelagic fish species listed in Table 2, neither of which substantially contribute to %N or %FO.

We propose that *D. gigas* routinely takes advantage of foraging opportunities in both ways discussed above. In Santa Rosalia a locally stable resource of mesopelagic micronekton represents a primary attraction to jumbo squid, but they still take advantage of unpredictable opportunities to forage on other neritic and small pelagic fishes. Archival tagging data indicate that jumbo squid tend to leave the tagging site on the shelf off Santa Rosalia after a few days and move over deeper offshore waters (Gilly et al. 2006). We suggest that these horizontal movements are associated with explorations for improved foraging grounds and that during such forays opportunistic foraging may be particularly common. A pattern like this has also been observed on the shelf outside Magdalena Bay on the Pacific coast, where jumbo squid consumed pelagic red crabs and an assortment of fishes as well as myctophids (Bazzino et al., submitted).

Relevance to *Dosidicus gigas* Diet in Other Locations

Samples in recent years have consistently shown that the mesopelagic micronekton (mainly myctophids) of the Guaymas Basin in the Gulf of California can sustain a population of *Dosidicus gigas* on a year-round basis since the fishery resumed in 1994 (Markaida and Sosa-

Nishizaki 2003; Markaida 2006; this study). It is thus likely that patterns observed in this core region of the central Gulf are relevant elsewhere. In particular, the balance between stable and opportunistic foraging is likely to be critical in determining how long jumbo squid will remain in a given area. The most extensive data set relevant to this question comes from the Pacific Ocean off California in conjunction with the recent northward range expansion of this species (Field et al. 2007). Jumbo squid off central California consume large numbers of myctophids and other small mesopelagic organisms, but they also forage heavily on a variety of fairly large fishes, including hake, rockfish (*Sebastes* spp.), anchovy, and sardine. Maximum size of prey items is also substantially larger in the more northern waters.

Although these fishes may be attractive prey, it is unlikely that foraging on such relatively slow-growing and long-lived species (relative to *D. gigas*) alone could be maintained on the long-term in a given locality. Indeed, a reciprocal relationship between hake abundance and jumbo squid abundance in Monterey Bay, California, has been suggested based on unmanned submersible operations over the last decade (Zeidberg and Robison 2007). Even in such highly productive areas, a diet of mesopelagic micronekton, particularly myctophids, is likely to be far more sustainable. Given the highly migratory nature of jumbo squid, opportunistic explorations from a relatively stable center would appear to be an effective strategy, both in the Guaymas Basin and elsewhere.

ACKNOWLEDGMENTS

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