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Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico

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Stomach contents of 533 jumbo squid, *Dosidicus gigas*, ranging between 14.5 and 87.5 cm dorsal mantle length were collected on a monthly basis in the central Gulf of California from November 1995 to April 1997. Fish prey were identified by sagittal otoliths, cephalopods by beaks and crustaceans by exoskeletal features. The diet was dominated by *Benthosema panamense*, an abundant near-shore nyctoepipelagic myctophid that forms dense aggregations. Another myctophid, *Triphoturus mexicanus*, several micronektonic squid, pelagic red crab and small pelagic fish such as northern anchovy and Pacific sardine played a secondary role. The largest differences in diet were due to spatial and monthly changes, while differences regarding squid size or sex were smaller. Prey size (averaging 5–7 cm) and prey number did not vary with size of jumbo squid. Jumbo squid in the slopes of the Guaymas basin feed on abundant schooling mesopelagic micronekton of annual nature with a quick response to environmental changes, which could partly explain the large annual fluctuations of this commercial resource.

INTRODUCTION

Cephalopods play an important role in the trophic structure of the world's marine ecosystems (Rodhouse & Nigmatullin, 1996). They are rapid, active predators that feed on live prey, mainly crustaceans, fish and other cephalopods and exhibit an ontogenetic succession in their feeding (Nixon, 1987; Hanlon & Messenger, 1996; Rodhouse & Nigmatullin, 1996). However, the difficulties associated with studying cephalopod diets have been stressed (Nixon, 1987).

Jumbo squid, *Dosidicus gigas* (D'Orbigny, 1835) (Ommastrephidae), is the largest (up to 100–120 cm dorsal mantle length, ML) and one of the most abundant nectonic squid and is endemic to the eastern Pacific (Nigmatullin et al., 2001). Between 1995 and 1997 a large scale artisanal jigging fishery for jumbo squid developed in the Gulf of California, with annual catches over 100,000 mtn. Squid was fished mainly in the central Gulf, off Guaymas from November to May and off Santa Rosalia from May to October (Markaida & Sosa-Nishizaki, 2001). Over 70% of jumbo squid catches were taken off Santa Rosalia during summer months.

Despite numerous reports on the stomach contents of jumbo squid (see reviews in Nesis, 1983; Clarke & Paliza, 2000; Nigmatullin et al., 2001), few papers give a detailed quantification of the diet. Nesis (1970) reported mainly myctophids (in 70.2% of the stomach), squid (mainly cannibalism) and plankton by frequency of occurrence in 266 jumbo squid, 20–59 cm ML, caught off South America. Fitch (1976) has been the only author to identify fish prey in the diet of jumbo squid based on otoliths. He found 100 fish, 20 mollusc and half a dozen crustacean species in more than 800 stomachs of squid 9–49 cm ML collected from California to Costa Rica.

Shchetinnikov (1986a,b, 1989) examined samples from Ecuador and Peru in 1981 and provided the most detailed account of jumbo squid feeding. Mature squid were found to feed mainly on nyctoepipelagic myctophids, although the dietary composition varied geographically, but not by sex (Shchetinnikov, 1986a,b). Dietary dominance by myctophids was related to productive waters, while in oligotrophic waters the incidence of less important prey or cannibalism increased (Shchetinnikov, 1986b).

First observations on jumbo squid feeding in the Gulf of California were made by Fitch (in Wormuth, 1976), who identified myctophid and gonostomatid otoliths in their stomach contents. Sato (1976) reported pelagic red crab (*Pleuroncodes planipes*), myctophids, anchovies, mackerel and several kinds of larvae in squid smaller than 40 cm ML. Ehrhardt et al. (1983) enumerated sardine (*Sardinops sagax*), mackerel (*Scomber japonicus*) and pelagic red crab as the main prey of jumbo squid in the Gulf of California in 1980. In a more detailed study based on 688 squid stomachs, Ehrhardt (1991) found that the importance of those prey and that of prey such as myctophids, shrimp postlarvae and cannibalism alternated on a monthly basis during the migration of jumbo squid within the Gulf. García-Domínguez & González-Ramírez (1988) found that fish remains, jumbo squid, large plankton and unidentified remains occurred in most of the stomachs of 138 jumbo squid ranging in size from 19.2–53 cm ML captured in the Gulf of California between 1980 and 1981.

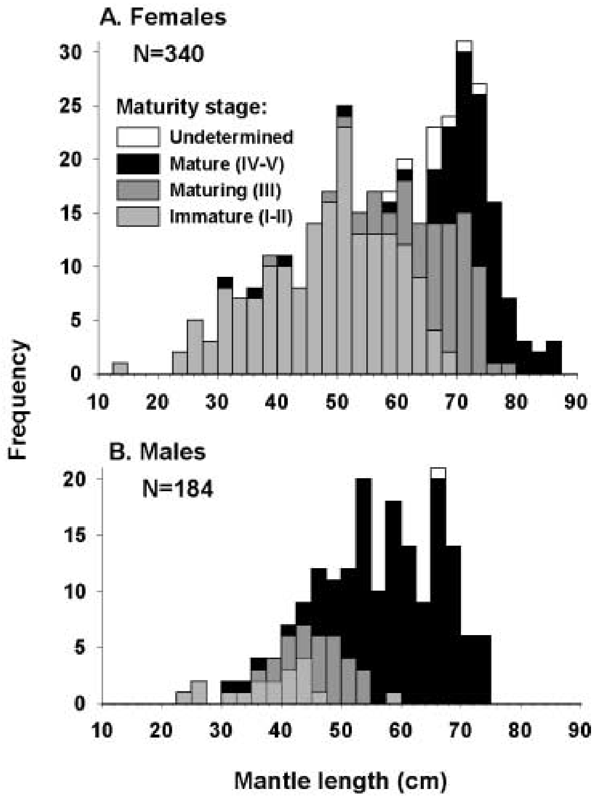

Figure 1. Size–frequency distribution of jumbo squid from the Gulf of California whose stomach contents were analysed for (A) females and (B) males, by stage of maturity.

Table 1. *Relationships between otolith length (OL) and total length (TL), standard length (SL) and body weight (BW, g) for* Benthosema panamense *and Pacific sardine, and between lower or upper beak rostral length (LRL or URL) and statolith length (SL) and dorsal mantle length (ML) for jumbo squid. All variables in mm.*

Relationship	r^2	N	Range
Benthosema panamense			
$TL=-3.3272+25.0114\ OL$	0.78	83	37–62.5 mm TL
$SL=-0.3755+18.935\ OL$	0.76	83	30–51.1 mm SL
$BW=0.0926\times OL^{2.9648}$	0.64	81	0.3–1.5 g BW
Pacific sardine *Sardinops sagax**			
$SL=26.07+57.34\ OL$	0.86	3007	102–213 mm SL
Jumbo squid *Dosidicus gigas*			
$ML=119.1+32.9\ LRL$	0.90	252	161–821 mm ML
$ML=129.8+30.5\ URL$	0.88	233	161–768 mm ML
$ML=103.8\times SL^{0.1954}$	0.78	513	108–875 mm ML

*, Relationship provided by Casimiro Quiñónez-Velázquez, Departamento de Pesquerías y Biología Marina, CICIMAR, La Paz, B.C.S. Personal communication.

Jumbo squid larger than 50 cm ML are under-represented in these studies. Excluding Shchetinnikov (1986a,b, 1989) and Fitch (1976, in Wormuth, 1976), the methodology for prey identification is not detailed in the rest of works. The objective of this study, therefore, is to provide a detailed description of the food sources and infer feeding habits of jumbo squid of the large-maturing form (up to 87 cm ML) captured in the Gulf of California. Temporal and spatial variation in the diet, as well as differences by sex and squid size were studied and specific information on common prey items is described.

MATERIALS AND METHODS

A total of 533 jumbo squid stomachs were collected on a monthly basis between November 1995 and April 1997 in the continental slope off both coasts of the central Gulf of California. Following the seasonal squid fishing pattern, samples from November to May were collected off Guaymas, while samples from July to October were taken off Santa Rosalia; in June 1996 samples were taken in San Pedro Martir basin and no samples were obtained during February and December 1996 (see figure 1 in Markaida & Sosa-Nishizaki, 2001). Monthly sample size ranged between 24 and 54 stomachs. Stomachs collected from November 1995 to August 1996 (298) were immediately preserved in buffered 10% formaldehyde, while 235 stomachs collected between September 1996 to April 1997 were kept frozen until their subsequent analysis in the laboratory.

For all squid ML (to the nearest mm) and body weight (BW, to the nearest 15 g) were measured. The sex was noted and maturity stage was assigned according to Lipiński & Underhill (1995). A subjective, visual stomach fullness index (FI) was assigned: 0, empty; 1, scarce remains; 2, half full; 3, almost full; and 4, completely full (Breiby & Joblin, 1985). Stomach contents were weighed to the nearest 0.1 g (SCW); then the weight of the stomach contents relative to body weight (Fullness Weight Index, FWI; Rasero et al., 1996) was calculated as:

$$FWI=\frac{SCW\times 100}{(BW-SCW)} \quad (1)$$

An estimation of the maximum value of this index was done as a regression fitted to the average of the two maximum FWI values of each 2.5 kg BW class. Comparisons for FI and FWI values among preservation method, month, squid sex and maturity different sizes were performed using an analysis of variance (ANOVA).

Stomach contents were screened through a 0.5-mm mesh sieve in order to retain prey remains useful for identification. Each sample was observed under a binocular microscope (×60–120) over a black and white background. Fish sagittal otoliths were identified by consulting the work of Fitch (1969a,b), Fitch & Brownell (1968) and Lavenberg & Fitch (1966). The otolith collection of the Department of Fish, Section of Vertebrates at Los Angeles County Museum of Natural History, California, was subsequently visited. Finally, unidentified otoliths were sent to William A. Walker (National Marine Mammal Laboratory, NMFS, Seattle, USA) for their examination. Cephalopod beaks were identified following Clarke (1986) and by comparing them with our personal reference collection. Pelagic gastropods were identified based on McGowan (1968). Crustaceans were identified by their exoskeleton; pelagic shrimp were identified following Hendrickx & Estrada-Navarrete (1996).

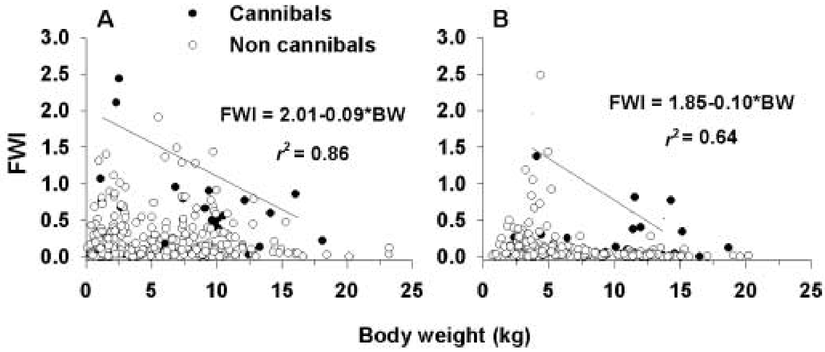

Figure 2. Stomach fullness of jumbo squid from the Gulf of California. Regression for their maximum FWI values by 2.5 kg body weight class interval for (A) formaldehyde preserved and (B) frozen stomachs.

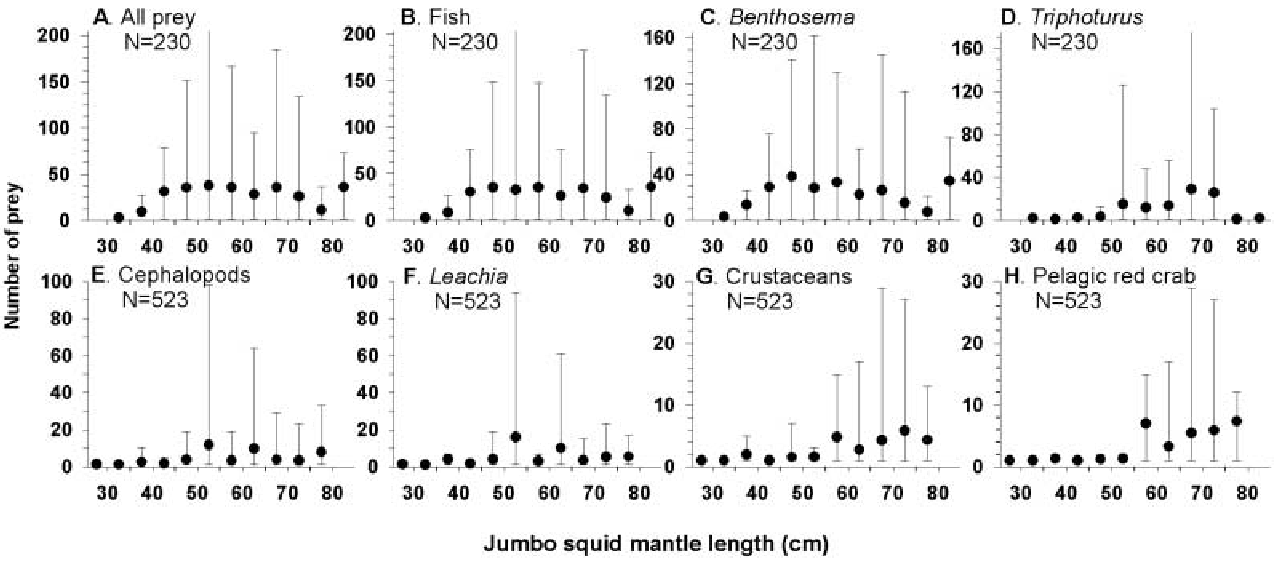

Figure 3. Variability of the average and range in number of the most important prey of jumbo squid from the Gulf of California for each 5 cm ML for (A) all prey; (B) all fish; (C) *Benthosema panamense*; and (D) *Triphoturus mexicanus* in 230 frozen stomachs and (E) all cephalopods; (F) *Leachia*; (G) all crustaceans and (H) pelagic red crab in 523 stomachs.

The number of consumed fish or cephalopods was estimated as the maximum number of right or left fish otoliths, or of upper or lower cephalopod beaks. The advanced degree of digestion of stomach contents generally impedes the exact and complete separation of prey for the purposes of weighing (Breiby & Jobling, 1985). Hence, only the most conspicuous prey items were weighed to the nearest 0.1 g. The monthly minimum sample size required to adequately describe the diet of jumbo squid in the Gulf of California was determined using the graphic method proposed by Hoffman (1979).

Frequency of occurrence, numeric and gravimetric (volumetric) methods were used to quantify the diet. Frequency of occurrence (%FO) was calculated as the percentage of jumbo squid that fed on a certain prey, number (%N) is the number of individuals of a certain prey relative to the total number of individual prey, and weight (%W) is defined as the weight of a certain prey relative to the total weight of all prey, expressed as a percentage (Cailliet, 1977). The index of relative importance IRI=(%N+%W)×(%FO) was calculated and graphs were plotted to illustrate monthly diet composition (Pinkas et al., 1971). Only prey species or taxa with IRI values >1% were included in plots.

Jumbo squid stomach contents were grouped by preservation method, squid sex and size, and fishing season to test for the effect of these variables on diet. Differences in prey numbers among squid groupings were analysed building $R \times C$ contingency tables and calculating G statistics (Crow, 1982),

$$G = 2 \times \sum_{i,j} X_{ij} \ln \left(X_{ij} / (X_i X_j / N) \right) \quad (2)$$

where X_{ij} is the number of prey of the i category ingested by the j squid category, X_i is the number of prey of the i category ingested by all squid, X_j is the total number of prey ingested by the j squid category, and N it is the total number of prey ingested by all squid. This statistic has a χ^2 distribution with $(R-1)\times(C-1)$ degrees of freedom.

Frequency of occurrence values among different squid groupings were compared by transforming them to proportions and performing a comparison of two or more proportions (Zar, 1999). Statistical analyses were considered significant if $P<0.05$, very significant if $P<0.01$ or highly significant if $P<0.001$.

For each frozen stomach, the length of up to 15 of the best preserved, least eroded, otoliths of each fish species

Table 2. *Summary of prey found in the stomach contents of jumbo squid from the Gulf of California by frequency of occurrence (FO), number and weight.*

	Stomach in formaldehyde (N=298)						Frozen stomach (N=235)					
	FO		Number		Weight		FO		Number		Weight	
Prey	FO	FO%	N	N%	g	W%	FO	FO%	N	N%	g	W%
PISCES	191	64.0	940	56.5	1104.4	29.3	202	85.9	5879	83.1	689.4	54.6
Myctophidae:	179	60.0	890	53.5	153.6	4.0	193	82.1	5701	80.6	263.4	20.8
Benthosema panamense	51	17.1	369	22.2	64.9	1.7	186	79.1	4768	67.4	201.4	15.9
Triphoturus mexicanus	2	0.6	2	0.1			63	26.8	881	12.4	8.0	0.6
Diogenichthys laternatus	1	0.3	1	0.06			10	4.2	36	0.5		
Bolinichthys longipes							6	2.5	11	0.1		
Diaphus sp.							2	0.8	2	0.02		
Unidentified Myctophidae	131	43.9	518	31.1			3	1.2	3	0.04		
Clupeidae:												
Sardinops sagax	14	4.6	22	1.3	97.1	2.5	26	11.0	53	0.7	37.8	2.9
Harengula thrissina							1	0.4	3	0.04		
Unidentified Clupeidae							2	0.8	2	0.02		
Engraulidae:												
Engraulis mordax							15	6.3	58	0.8	40.5	3.2
Bregmacerotidae:												
Bregmaceros bathymaster							9	3.8	10	0.1		
Macrouridae:												
Coryphaenoides sp.							1	0.4	1	0.01		
Moridae:												
Physiculus sp.							4	1.7	4	0.05		
Carangidae:												
Oligoplites sp.	3	1.0	3	0.1	131.4	3.4	2	0.8	4	0.05	80.9	6.4
Unidentified Carangidae							1	0.4	1	0.01		
Belonidae	3	1.0	3	0.1								
Scombridae:												
Scomber japonicus	3	1.0	3	0.1	9.0	0.2						
Congridae							3	1.2	3	0.04		
Photichthyidae:												
Vinciguerria lucetia							2	0.8	8	0.1		
Bathylagidae:												
Leuroglossus stilbius							1	0.4	5	0.07		
Argentinidae:												
Argentina sialis							1	0.4	1	0.01		
Trichiuridae							2	0.8	2	0.02		
Batrachoididae:												
Porichthys sp.	1	0.3	1	0.06	2.1	0.05	1	0.4	4	0.05	30.4	2.4
Scopelarchidae							2	0.8	2	0.02		
Merlucciidae:												
Merluccius angustimanus	1	0.3	1	0.06								
Priacanthidae:												
Priacanthus sp.							1	0.4	1	0.01		
Melamphaidae:												
Melamphaes sp.							1	0.4	1	0.01		
Gobiidae							1	0.4	1	0.4		
Unidentified Teleostei	16	5.3	17	1.0	2.1	0.05	12	5.1	14	0.1		
CEPHALOPODA	82	27.5	280	16.8			81	34.4	538	7.6	37.8	2.9
Cranchidae:												
Leachia sp.	38	12.7	158	9.5			42	17.8	338	4.7		
Enoploteuthidae:												
Abraliopsis affinis	13	4.3	14	0.8			12	5.1	14	0.1		
Gonatidae:												
Gonatus sp.	9	3.0	10	0.6			46	19.5	140	1.9		
Gonatus californiensis	1	0.3	1	0.06								

Continued

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Table 2. *Continued.*

	Stomach in formaldehyde (N=298)						Frozen stomach (N=235)					
	FO		Number		Weight		FO		Number		Weight	
Prey	FO	FO%	N	N%	g	W%	FO	FO%	N	N%	g	W%
CEPHALOPODA (*Continued*)	82	27.5	280	16.8			81	34.4	538	7.6	37.8	2.9
Ancistrocheiridae:												
Ancistrocheirus lesueurii							3	1.2	3	0.04	36.5	2.8
Loliginidae?	1	0.3	1	0.06								
Octopodidae:												
Octopus sp.	6	2.0	7	0.4			15	6.3	38	0.5		
Argonautidae:												
Argonauta sp.	1	0.3	1	0.06								
Unidentified Cephalopoda	37	12.4	84	5.0			5	2.1	5	0.07		
Dosidicus gigas	77	25.8	77	4.6	1330.4	35.4	62	26.3	62	0.8	589.5	46.7
Juveniles <4 cm ML	4	1.3	4	0.2								
OTHER MOLLUSCA												
Thecosomata:												
Cavolinia sp.	1	0.3	1	0.06			4	1.7	7	0.09	0.2	0.01
Clio sp.							1	0.4	2	0.02		
Unidentified Gastropoda							4	1.7	4	0.05		
Unidentified Pelecypoda	4	1.3	5	0.3			28	11.9	69	0.9		
CRUSTACEA	96	32.2	351	21.1	794.4	21.1	32	13.6	495	7.0	99.1	7.8
Galatheidae:												
Pleuroncodes planipes	60	20.1	284	17.0	742.8	19.7	12	5.1	30	0.4	83.9	6.6
Pandalidae:												
Plesionika sp.	11	3.6	27	1.6	48.2	1.2						
Scyoniidae:												
Scyonia sp.	5	1.6	7	0.4	3.2	0.08						
Unidentified Pasiphaeidae	1	0.3	1	0.06								
Unidentified Caridea	1	0.3	1	0.06	0.2	0.005						
Unidentified shrimp	2	0.6	2	0.1								
Unidentified Brachyura							3	1.2	3	0.04	10.9	0.8
Euphausiacea							3	1.2	402	5.6	4	0.3
Copepoda	2	0.6	2	0.1								
Isopoda	2	0.6	2	0.1								
Amphipoda	2	0.6	3	0.1								
Ostracoda	1	0.3	1	0.06								
Unidentified Crustacea	14	4.6	21	1.2			18	7.6	60	0.8	0.3	<0.01
Hydrozoa?							1	0.4	3	0.04		
Other items	7	2.3	7	0.42	45.9	1.2	9	3.8	9	0.1	2.9	0.2
UOM[1]	154	51.6			1279.8	34.0	71	30.2			134.5	10.6
TOTAL	298		1661		3757.1		235		7068		1261.7	

[1], Unidentified organic matter.

were measured to the nearest 0.1 mm. The size of ingested fish was calculated using otolith length (OL) to standard length (SL) relationships for each species or genus (Spratt, 1975; Aurioles-Gamboa, 1991). The relationships used for the myctophid *Benthosema panamense* and Pacific sardine are listed in Table 1. Rostral lengths of squid lower beaks (LRL) and lower hood lengths of lower octopod beaks (LHL) from all stomachs 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

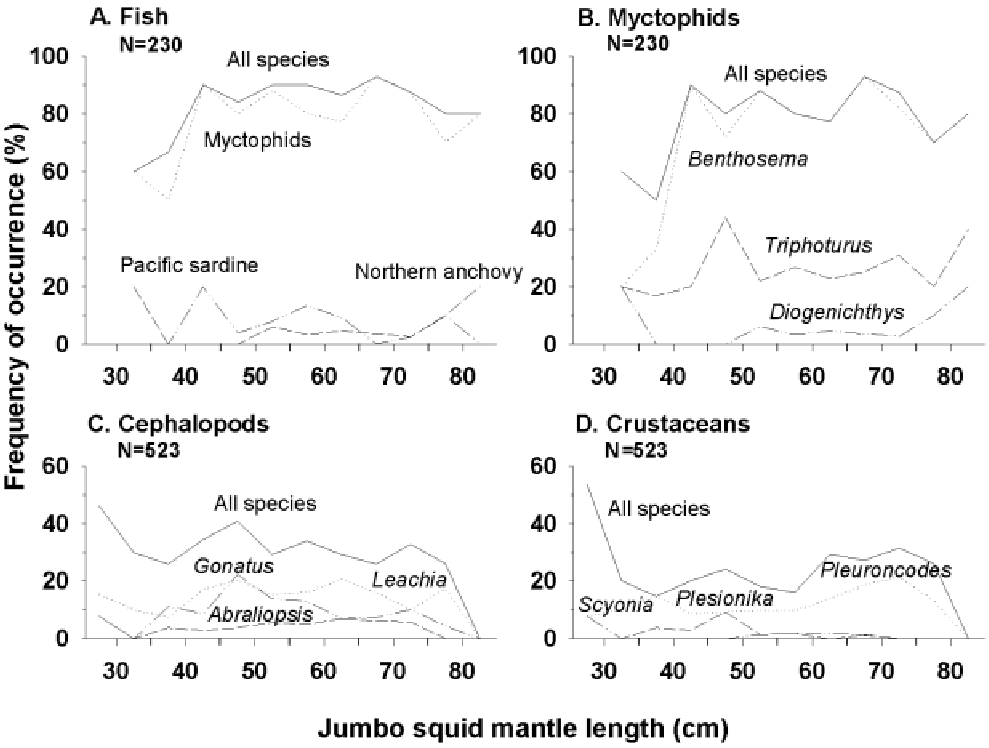

Figure 4. Variability of the frequency of occurrence of the most important prey of the jumbo squid from the Gulf of California for each 5 cm ML for (A) fish and (B) myctophids in 230 frozen stomachs, and (C) cephalopods and (D) crustaceans in 523 stomachs.

estimated using the relationships provided by Clarke (1986) and Wolff (1984). The MLs of cannibalized jumbo squid were estimated based on beak rostral lengths and statolith length relationships (Table 1).

RESULTS

The size of the squid analysed for stomach contents varied between 14.5 and 87.5 cm ML, with an average of 57.3 ±13.3 cm ML (Figure 1). There was a highly significant variation in monthly squid size ($F_{15,508}$=18.13; $P<0.001$). The overall sex ratio was 1.8:1 in females to males and no monthly variation was found (χ^2=10.8, df=28, $P>0.05$). Of the females, 180 were immature, 71 maturing and 80 mature, while for males 18 were immature, 27 maturing and 138 mature (Figure 1).

Stomach fullness

Stomachs preserved in formaldehyde showed higher average FI values (2.15 ±1.44) than frozen stomachs (1.86 ±1.03) (ANOVA, $F_{1,531}$=8.58, $P<0.01$). There were no significant differences in monthly FI between stomachs preserved with formaldehyde and frozen. The FWI of 298 stomachs preserved in formaldehyde was higher (0.26 ±0.12) than in the 236 frozen ones (0.13 ±0.07), ($F_{1,523}$=23.1, $P<0.001$). There were highly significant monthly differences in FWI between stomachs preserved in formaldehyde ($F_{8,288}$=6.03, $P<0.001$), but not for frozen stomachs. No seasonal patterns were observed.

Considering squid size, there were no differences in FI between 5 cm ML size-classes for stomachs preserved in formaldehyde, or frozen. Likewise no differences were found for FWI among size-classes for samples fixed in formaldehyde, or frozen. There were also no significant differences for each method of preservation between sexes or maturity stages in FI and FWI values (ANOVA, $P>0.05$ in all cases).

The maximum weight of the stomach contents expressed relative to squid BW decreased with size (Figure 2). The highest FWI values were found in 11 cannibalistic squid not shown in the figure. Their stomachs had jumbo squid remains that weighed between 350 g and 2.1 kg, which represented between 4.1 and 17.8% of the predator's BW.

Sample size

Hoffman's graphic method suggested that a minimum monthly sample size of 20–25 stomachs for formaldehyde-preserved stomachs and 20 for frozen stomach was adequate. Hence we considered that the collected sample sizes used were large enough to adequately describe the diet of jumbo squid. Shchetinnikov (1986a) also estimated that 20 stomachs per sample were enough to describe the diet of the jumbo squid off Peru.

General description of the diet

For stomachs preserved in formaldehyde, 46 (15.4%) did not have identifiable prey remains and 21 were totally empty or contained only food traces. In frozen stomachs, 18 (7.6%) had no identifiable remains and ten were empty or with food traces.

The trophic spectrum of jumbo squid from the Gulf of California consisted of three main groups: fish, molluscs and crustaceans. Stomach contents were usually well digested and prey were mostly represented by their hard remains. In stomachs preserved in formaldehyde, the

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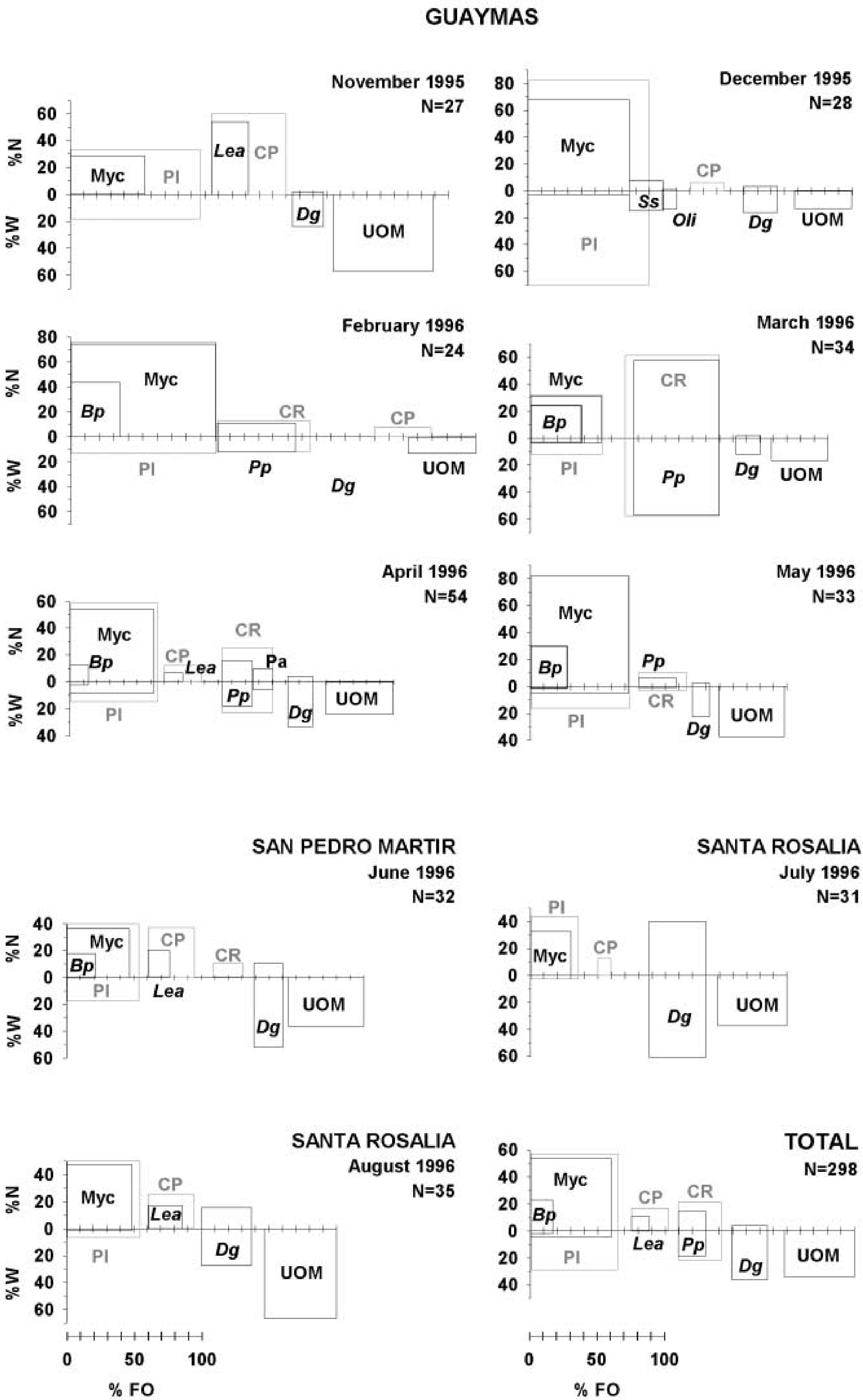

Figure 5. Monthly composition by percentage number (%N), weight (%W) and frequency of occurrence (%FO) of those preys found in stomach contents of jumbo squid collected in the Gulf of California from November 1995 to August 1996 and preserved in formaldehyde. Myc, Myctophidae; *Bp*, *Benthosema panamense*; *Ss*, *Sardinops sagax*; *Oli*, *Oligoplites*; *Lea*, *Leachia* sp.; *Pp*, *Pleuroncodes planipes*; Pa, Pandalidae; *Dg*, *Dosidicus gigas* and UOM, unidentified organic matter. Large prey groups in grey: PI, Pisces; CP, Cephalopoda; CR, Crustacea.

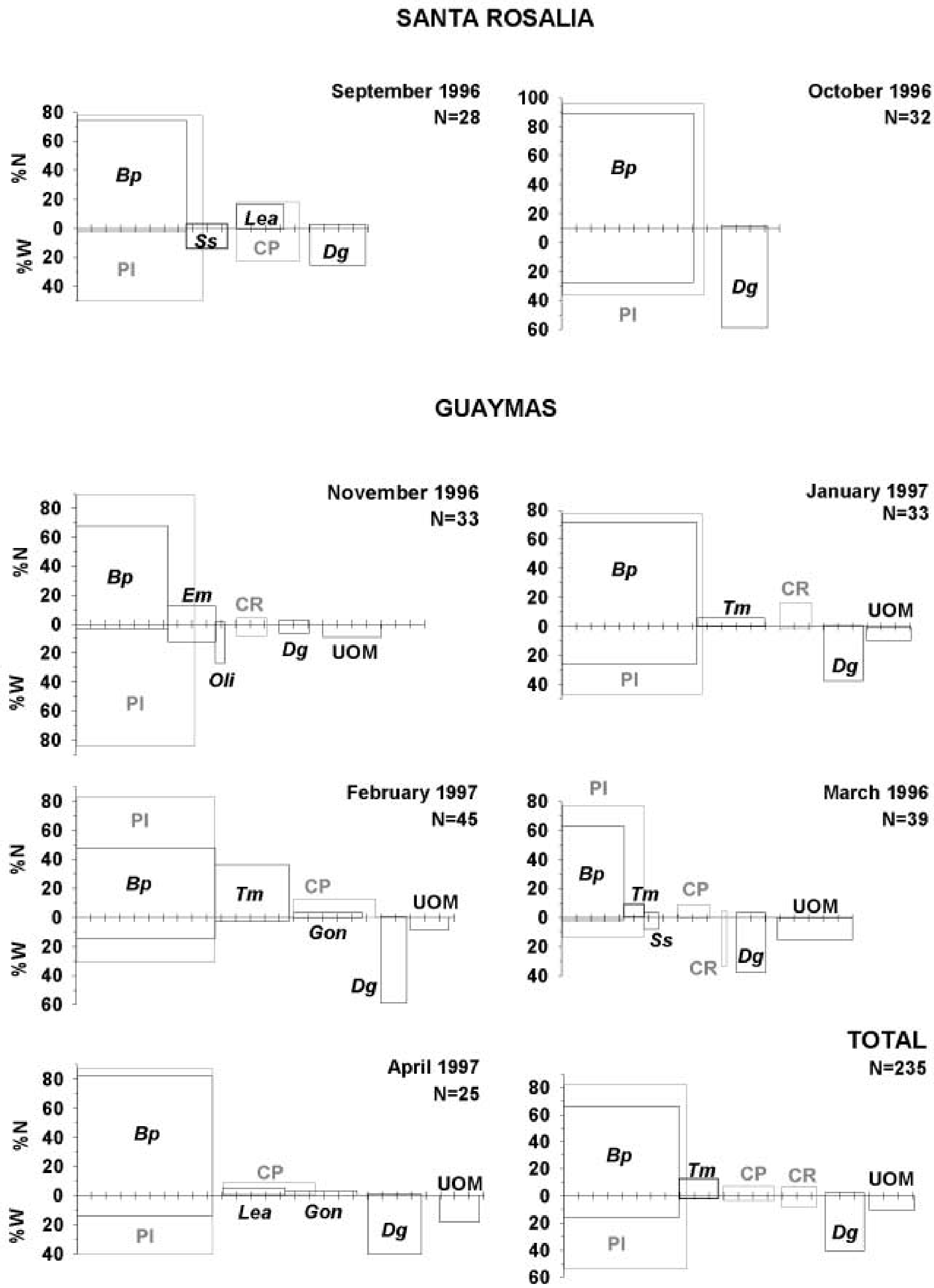

Figure 6. Monthly composition by percentage number (%N), weight (%W) and frequency of occurrence (%FO) of those preys found in stomach contents of jumbo squid collected in the Gulf of California from September 1996 to April 1997 and preserved frozen. *Bp*, *Benthosema panamense*; *Tm*, *Triphoturus mexicanus*; *Ss*, *Sardinops sagax*; *Em*, *Engraulis mordax*; *Oli*, *Oligoplites*; *Lea*, *Leachia* sp.; *Gon*, *Gonatus* sp.; *Dg*, *Dosidicus gigas*; and UOM, unidentified organic matter. Large prey groups in grey: PI, Pisces; CP, Cephalopoda; CR, Crustacea.

number of fish had to be estimated mostly based on the presence of eye lenses (63% FO). Otoliths (28% FO) were often forming conglomerates, due to the eroding effect of formaldehyde. The use of formaldehyde to preserve stomach contents in dietary studies has been highly criticized (Fitch & Brownell, 1968; Jobling & Breiby, 1986) and stomachs preserved in formaldehyde underestimated the number and frequency of occurrence of fish in the diet. Vertebrae were counted only in 4% of the cases. Scales were useful only for identifying Pacific sardine, *Sardinops sagax*, and leatherjack, *Oligoplites* sp. By contrast, in frozen stomachs practically all the fish were identified using sagittal otoliths. Squid were identified using beaks in 89.2% of stomachs containing squid remains, or classified as unidentifiable cephalopods based on the lenses in the remaining stomachs.

The diet of jumbo squid was dominated by myctophids, which occurred in 64% of formaldehyde-preserved stomachs and accounted for 56.5% by number of all the

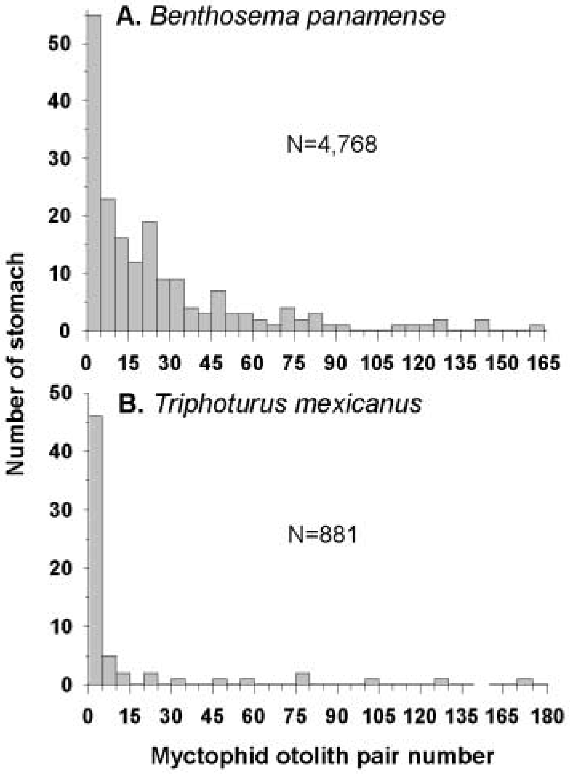

Figure 7. Frequency of stomach by myctophid otolith pair number occurrence for (A) *Benthosema panamense* in 186 and (B) *Thiphoturus mexicanus* in 63 jumbo squid frozen stomachs.

prey items (Table 2). However, most myctophids (58%) could not be specifically identified. In frozen stomachs most myctophids were identified as *Benthosema panamense*, which was present in 79% of the sample and represented 67.4% of all prey. Therefore, it is probable that most unidentified myctophids in the formaldehyde-preserved stomachs belonged to this species. Another myctophid, *Triphoturus mexicanus*, accounted for 12% of all prey by number and occurred in 27% of frozen stomachs.

Epipelagic fish were represented by five families, including Pacific sardine and northern anchovy. They accounted for 2.2% of all fish prey and occurred in 12.3% of all stomachs (Table 2). Five families of demersal or benthic fish were found and were represented by 11 individuals in 8 stomachs (1.5%).

Among cephalopods, micronektonic squid as the cranchiid *Leachia* sp. and, to a lesser extent, the gonatid *Gonatus* sp. were the most important (Table 2). Most of the unidentified squid lenses probably belong to *Leachia* sp. The pelagic red crab, *Pleuroncodes planipes*, was the only consistently abundant crustacean. It occurred in 20% of the stomachs preserved in formaldehyde and accounted for 17% of all prey and 20% of the total weight of the stomach contents (Table 2). A stomach of a 73.9 cm ML male squid collected in January 1997 contained roughly 400 euphausiid mandibles and was excluded from subsequent analysis.

Unidentified organic matter was observed in half of all stomach preserved in formaldehyde, and comprising up to 34% of the weight of their contents (Table 2). Evidence of cannibalism was found in 26% of all stomachs analysed. All of them were single occurrences, representing 35–46% by weight of all stomachs. Other items found included algae, fishing material and fragments from the marine bottom.

Unidentified species of small bivalves and gastropods (1–1.2 mm length), probably planktonic larvae, were considered secondary or transitory prey. These are mesoplanktonic organisms introduced from the prey of squid (Nigmatullin & Toporova, 1982). They were almost always associated with the presence of *B. panamense* in our stomach samples. It is probable that smaller crustaceans (copepods, anphipods, isopods and ostracods) were also secondary prey (Shchetinnikov, 1986a,b, 1989).

Dietary variations

In order to test for differences in the number and frequency of occurrence of jumbo squid prey, the following prey species or taxa were considered: Myctophids (*B. panamense*, *T. mexicanus*), other fish, squid (*Leachia* sp., *Gonatus* sp.), other cephalopods, pelagic red crab, other crustaceans and jumbo squid.

By preservation type

Formaldehyde-preserved and frozen stomachs differed significantly in prey number for all prey types ($G \geqslant 11$, $P<0.01$, df=6-1). Up to six times more fish prey were counted from frozen stomachs than in those preserved in formaldehyde, due to its eroding effect on fish otoliths (Table 2). This effect is negligible in chitinous remains, so differences in cephalopod and crustacean numbers could not be due to preservation method. Frozen stomachs had a higher occurrence of fish, including myctophids, (Table 2; $Z=5.5$, $P<0.001$), whereas the occurrence of crustaceans, including pelagic red crab, ($Z=4.9$, $P<0.001$) and unidentified organic matter ($Z=4.9$, $P<0.001$) was lower than for formaldehide-preserved stomachs.

By sex

Females were larger than males (58.2 cm ML vs 55.8 cm ML; $t=1.97$, df=522; $P<0.05$). All species of squid prey (with the exception of cannibalism) were most numerous in males ($G>45$, $P<0.001$, gl=6-4). In frozen stomachs females contained more *T. mexicanus* ($G=7.84$, $P<0.05$, gl=2). In males %FO for *Leachia* sp. was higher ($Z=3.1$, $P<0.01$).

By predator size

Variability in the number of prey in 5 cm ML size-classes of jumbo squid was high for all prey species (Figure 3). Hence, no differences were noted in prey number with squid size for any prey, except for *Leachia* sp. (Kruskal–Wallis test, $P>0.05$ in all prey species). However, the *G*-test revealed that larger squid (>65 cm ML) feed on a larger number of *T. mexicanus* and crustaceans, including pelagic red crab ($G>291$, $P<0.001$, df=12-16). Medium size squid (50–65 cm ML) feed heavily on more *Leachia* sp. and other cephalopods ($G>12.9$, $P<0.05$, df=6-4).

There was no great variation in the%FO of fish prey among size groups (Figure 4A,B). *Benthosema panamense* was less frequent in the stomachs of small squid (<50 cm ML) ($\chi^2=8.4$, $P<0.05$, df=2). Northern anchovy and *Diogenichthys laternatus* only appeared in the stomachs of squid>45 cm ML. There was no trend in the %FO of

Table 3. *Hard remains sizes and dimensions estimated from them for prey of jumbo squid in the Gulf of California.*

					Estimated prey dimensions						
		Otolith length, mm			Standard length, mm			% Jumbo squid ML			
Prey	Number	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Weight, g
Fish											
Benthosema panamense	1096	1.93	0.22	0.8–2.8	45[1]	5.5	21.6–66.7	8.1	1.7	3.4–20	0.12–1.9
Triphoturus mexicanus	235	0.97	0.15	0.6–1.3							
Diogenichthys laternatus	14	0.96	0.09	0.8–1.2							
Engraulis mordax	35	3.7	0.3	3.0–4.3	114	10	91–134	20.4	2	16–25	
Sardinops sagax	14	2.1	0.5	1.4–3	151	28	106–198	26	6.5	17–40	
Bregmaceros bathymaster	9	1.24	0.27	0.9–1.7							
Porychthis sp.	3	5.7	0.1	5.6–5.8	121	2.9	118–124	23.5	0.5	23–24	17–20
Merluccius angustimanus	1	7.7			143			21.1			31.7
		Lower rostral length, mm			Mantle length, mm						
		Mean	SD	Range	Mean	SD	Range				
Cephalopod											
Leachia sp.	265	0.42	0.1	0.1–0.8	47.4	7.2	25–72	8.1	1.9	3.4–18	0.007–1
Gonatus sp.	105	0.74	0.27	0.3–1.9	27.1	5.2	17–49	5	1.4	2.4–13.6	0.01–4.2
G. californiensis	1	8.1			303			48			550
Abraliopsis affinis	17	1.07	0.14	0.8–1.4	30.4	3	22–36.7	5.4	1.5	3.7–11.2	0.8–4
Ancistrocheirus lesueurii	3	3.72	1.2	2.7–3.3	110	52	68–168	19.1	4.3	14–23	28–283
Octopus sp.	32	0.45[2]	0.15	0.2–0.8							

[1], Total length, mm; [2], Lower hood length, mm.

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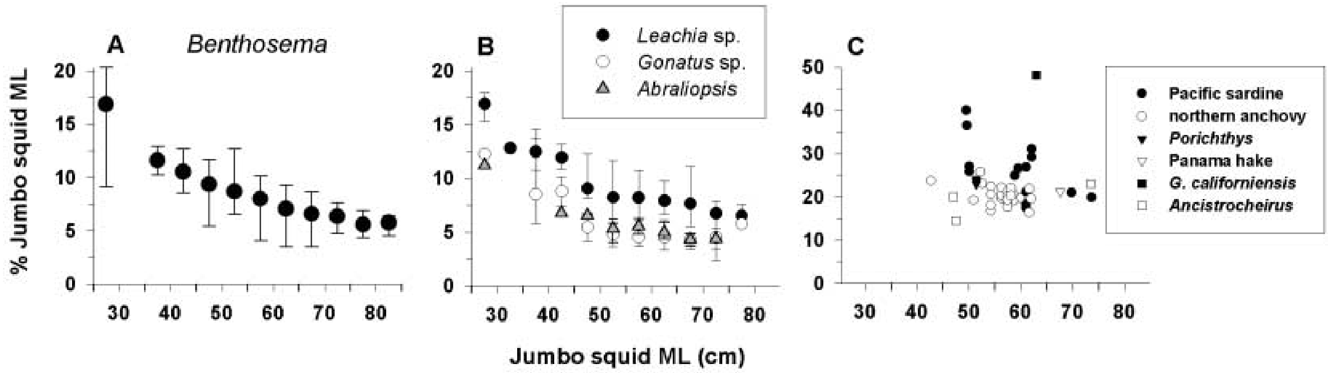

Figure 8. Variation of the relative size (% jumbo squid ML) of the most important preys for each 5 cm ML of jumbo squid: (A) total length of myctophid *Benthosema panamense*; (B) ML of squid *Leachia* sp., *Gonatus* sp. and *Abraliopsis affinis*; and (C) standard lengths of northern anchovy, Pacific sardine, *Porichthys* sp. and Panama hake, and ML of squid *G. californiensis* and *Ancistrocheirus lesueurii*.

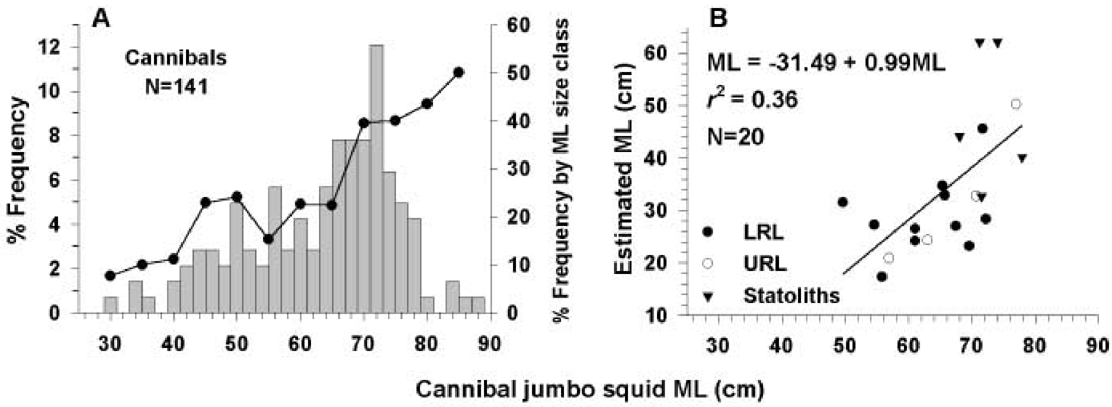

Figure 9. Cannibalism in jumbo squid from the Gulf of California: (A) Size–frequency distribution of cannibal jumbo squid and percentage of cannibal jumbo squid in relation of all squid for each 5 cm ML; and (B) relationship between the size of the cannibal jumbo squids and the estimated size of cannibalized jumbo squid. Estimations made from beak lower rostral (LRL), upper rostral (URL) and statolith lengths.

cephalopod prey species with size (Figure 4C). The frequency of shrimp (*Scyonia* and *Plesionika*) declined with jumbo squid size, while the pelagic red crab increased in frequency in the diet of squid > 65 cm ML (χ^2=16.8, P<0.01, df=2) (Figure 4D).

Monthly variations in diet

Myctophids dominated the diet of jumbo squid in most months. In stomachs preserved in formaldehyde (Figure 5), the monthly FO varied between 29 and 100% and their number between 27 and 81%. Cephalopods were present in most of the months. In November 1995, the squid *Leachia* sp. was the most numerous prey (52%N) and in June 1996 cephalopods were also frequent and numerous (34 and 37%N, respectively). Pelagic red crab was important during spring (February–May) of 1996; in March it was the dominant prey (64%FO, 60%N and 58%W) (Figure 5).

In frozen stomachs the dominant species, *B. panamense*, ranged between 43–94%FO and 47–89%N (Figure 6). *Triphoturus mexicanus* was second in importance during 1997 off Guaymas, mainly in February (51%FO and 36%N). Northern anchovy was only important in the diet during November 1996 and Pacific sardine appeared secondarily in almost every month, with maximum occurrences in December 1995, September 1996 and April 1997 (24–28%FO), while its weight never exceeded 14%. Cephalopods were of some importance in September 1996 (Figure 6).

Spatial variation

The diets of jumbo squid of similar size range captured off Guaymas and Santa Rosalia were compared. Stomachs collected off Guaymas contained a larger number of crustaceans (including pelagic red crab) and cephalopods (except *Leachia* sp.) (G>18, P<0.001, df=7-3). In frozen stomachs, they also presented more remains of *T. mexicanus* (G=368, P<0.001, df=6). Off Guaymas beaks of 140 individuals of *Gonatus* sp. were found in 46 stomachs, while off Santa Rosalia this squid was absent. Off Guaymas, the frequencies of *T. mexicanus*, cephalopods (excluding *Leachia* sp.) and crustaceans (including pelagic red crab) were higher than off Santa Rosalia (Z>2.1, P<0.05), while the incidence of cannibalism was lower (23% vs 33%).

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Prey number

Jumbo squid fed mainly on schooling prey. The average number of identifiable prey in a frozen stomach was 31.2 ±39.6, and a maximum of 205 (126 *T. mexicanus* and 77 *B. panamense* otolith pairs). The distribution of frequencies of otolith pair numbers for both myctophids is shown in Figure 7. Half of Pacific sardine occurrences were of more than one individual (up to 8 sardines). Eight northern anchovy occurrences were composed of three or more individuals (maximum of 14). In half of *Leachia* sp. occurrences of three or more individuals were found, and in 10 stomachs between 10 and 94 beak pairs were counted. Five to 14 *Gonatus* sp. beak pairs were found in 7 stomachs. Most occurrences of *Abraliopsis affinis* and pelagic red crab were single, although in 16 stomachs between 9 and 29 crabs were counted.

Prey size

Fish otoliths and cephalopod prey beak size dimensions and estimated prey sizes are shown in Table 3. Most of the common prey of jumbo squid (mesopelagic micronektonic myctophids and cephalopods) were small, averaging 5–7 cm and representing only 5–8% of jumbo squid ML (Table 3). Uncommon neritic fish prey and other mesopelagic squid were of larger sizes (10–15 cm, representing 20–25% of jumbo squid ML).

In general, no significant differences were found in prey size between jumbo squid grouped in 5 cm ML size intervals. For *T. mexicanus*, significant differences were found in otolith length among jumbo squid size-classes (ANOVA, $F=7.95$, $P<0.001$), although no significant correlation was detected among both variables ($r^2=0.09$, $P=0.32$). For northern anchovy, the correlation with squid size was very significant but weak ($r^2=0.16$, $P<0.01$). A poor correlation has often been found between cephalopod size and their prey size (Rodhouse & Nigmatullin, 1996).

There was a significant negative correlation between the mean relative size of prey and jumbo squid size. This was particularly true for *B. panamense* ($r^2=0.86$, $P<0.001$; Figure 8A) and the three micronektonic squid species ($r^2=0.6$–0.8, $P<0.01$; Figure 8B). For northern anchovy and Pacific sardine, the correlations were weaker ($r^2=0.2$–0.39, $P<0.05$; Figure 8C). The relative size of the most common jumbo squid prey decreased from 10–15% at 25–35 cm ML to 4–5% in squids 75–85 cm ML.

Cannibalism

The frequency of cannibalism increased with jumbo squid size (Figure 9A). Cannibalism was more frequent in females than males (29% vs 20%; $Z=2.15$, $P<0.05$). However this could be due to the larger size of females. When this size difference was not present, as for formaldehyde-preserved stomachs ($t=0.84$, $df=294$; $P>0.05$), the frequency of cannibalism was similar for both sexes (26% vs 25%; $Z=0.08$, $P>0.05$). There was a weak although highly significant correlation between squid size and that of its cannibalized prey ($r^2=0.36$, $P<0.001$, $N=20$) (Figure 9B). The size of cannibalized jumbo squid prey ranged between 27 and 87% of predator size (mean of 51 ±16%) and no correlation was detected between this relative size and the size of cannibal squid ($r^2=0.12$, $P=0.12$, $N=20$).

DISCUSSION

Stomach fullness

The high variability in stomach fullness and content weight observed in this study lead to a lack of significant differences based on squid size, sex, sexual maturity or season. During the night one to two feeding peaks have been detected in jumbo squid (Bazanov, 1986; Koronkiewicz, 1988) and stomach fullness may depend primarily on time they were caught.

Large incidences of empty stomach have been attributed to a high digestion rate (Baral, 1967; Ehrhardt et al., 1983). However, since jigs are an active fishing gear that depends on squid voracity, those captured could be hungrier and have a higher incidence of empty stomachs than satiated squid that do not attack the jigs. The stomach content weight was comprised of cannibalized squid and unidentified organic matter. The most common prey such as micronektonic myctophids and squid, however, had not probably been recently ingested.

It is possible that the otolith number found in the stomachs of jumbo squid represents several meals. Cephalopod gastric fluids are weak and otoliths immersed for two days show no evidence of erosion (Jobling & Breiby, 1986). Otoliths were commonly observed in the jumbo squid rectum, suggesting that they are evacuated from the stomach rather than retained until its complete digestion. The maximum number of otoliths per stomach did not vary consistently with jumbo squid size. This may be an indication that otoliths and other prey hard remains are frequently evacuated from the stomach.

Myctophids as prey

We found that myctophids dominate the diet of jumbo squid on the near-shore continental slope of the Guaymas basin. It is known that oceanic ommastrephid squid of medium size (⩽30–45 cm ML) feed mainly on myctophids (Filippova, 1974; Wormuth, 1976). Examples are: *Ommastrephes bartramii* (Gaevskaya & Nigmatullin, 1976; Araya, 1983; Lipiński & Linkowski, 1987), *Sthenoteuthis oualaniensis* (Nigmatullin et al., 1983; Shchetinnikov, 1992; Chesalin, 1994), *S. pteropus* (Nigmatullin & Toporova, 1982; Chesalin, 1985), and *Martialia hyadesi* (Rodhouse et al., 1992). Rodhouse & Nigmatullin (1996) have suggested that in the open ocean, epipelagic ommastrephids are possibly the main predators of myctophids.

Large-size oceanic ommastrephids feed on larger teleosts. Large females of *S. pteropus* (36–65 cm ML) and *O. bartrami* of 50–85 cm ML from the Atlantic feed on flying fish, deep water fish (10–30 cm SL), squid and large shrimp (C.M. Nigmatullin, personal communication). Jumbo squid ⩾50 cm ML from the eastern tropical Pacific feed on myctophids and juvenile exocoetids of same the maximum size (W.A. Walker, personal communication). These observations suggest that the size range of prey or the trophic niche breadth increases with squid growth (Shchetinnikov, 1989; Rodhouse & Nigmatullin, 1996). However, this was not observed in this study because large jumbo squid kept feeding on myctophids.

Myctophids from the Gulf of California

The Gulf of California offers a contrasting environment to its inhabitants, with a high productivity and extremely harsh conditions, including a pronounced oxygen minimum of 0.1–0.2 ml l^{-1} at 400–800 m depths (Moser et al., 1974). This leads to a depauperate mesopelagic ichthyofauna, largely dominated by *Triphoturus mexicanus*, whereas *Diogenichthys laternatus* and *Benthosema panamense* are next in abundance (Lavenberg & Fitch, 1966; Robison, 1972; Brewer, 1973; Moser et al., 1974). *Triphoturus mexicanus* belongs to the 'inactive' type of myctophid and toward its lower depth limit is often lethargic (Barham, 1971). In the Gulf of California it is found at the oxygen minimum layer during the daytime, whereas at night emerge less aggregated to the upper 100 m (Robison, 1972). *Benthosema panamense* belongs to the 'active' (Barham, 1971) or 'nyctoepipelagic' (Parin, 1968) myctophid type. In the Gulf of California it occurs between 200–300 m depth during the day, probably avoiding the oxygen minimum layer. At night, it migrates to the upper 100 m, and is the only mesopelagic fish commonly distributed above the thermocline (Robison, 1972; Moser et al., 1974). Robison (1972) considers *B. panamense* and *T. mexicanus* from the Gulf of California as the two extremes of the active–inactive types described by Barham (1971), which could be the basis of jumbo squid feeding preference for the former.

Nesis (1970, 1983) postulated that jumbo squid feed on any prey that moves as long as it is abundant and of the appropriate size. Bennett (1978) noted that squid prefer mobile prey, regardless of size or colour. Active myctophids are captured by squid following repeated attacks (Barham, 1971). In contrast, the immobile vertical orientation and lethargic behaviour of *T. mexicanus* perhaps has a mimetic function (Barham, 1971), or the absence of movement could be unattractive for jumbo squid. Perhaps inhabiting the oxygen minimum layer helps avoid predation.

Most myctophids identified from the stomach contents of medium size jumbo squid from other areas are also known to be nyctoepipelagic, like *Symbolophorus evermanni*, *Myctophum* spp., *Hygophum* spp., *Benthosema* spp. and *Gonichthys tenuiculus* (Nesis, 1970; Wormuth, 1976; Shchetinnikov, 1986a,b, 1989). Similar myctophids have been found in the diet of other oceanic ommastrephids (Wormuth, 1976; Nigmatullin & Toporova, 1982; Nigmatullin et al., 1983; Chesalin, 1985, 1994; Lipiński & Linkowski, 1987; Shchetinnikov, 1992).

However, the giant form of *Sthenoteuthis oualaniensis* (up to 65 cm ML) from the Arabian Sea, actively feeds in the oxygen minimum layer (350–400 m) during the day on lethargic, motionless myctophids (Nesis, 1993; Chesalin, 1994). Formation of dense aggregations of myctophids (Gjøsæter, 1981) could be the main feeding preference for large oceanic ommastrephids (C.M. Nigmatullin and K. Nesis, personal communication). This reflects the opportunistic nature of squid feeding (Rodhouse & Nigmatullin, 1996). *Benthosema panamense* forms the most compact aggregations in the eastern tropical Pacific (Alverson, 1961; Ahlstrom, 1969; Barham, 1971). Hundreds to thousands of individuals have been counted in the stomach contents of predators (Alverson, 1963; Fitch & Brownell, 1968). As a near-shore lanternfish (Wisner, 1974), *B. panamense* could be the most abundant myctophid on the continental slopes of the central Gulf of California where jumbo squid inhabit.

Other prey

Beak measurements of micronektonic squid found indicated juveniles or subadults of epipelagic habits, as *Leachia* sp. Most *Gonatus* are mesopelagic squid with a limited vertical migration, while *Abraliopsis* spp. migrate to 50–100 m at night, where they disperse (Roper & Young, 1975). This observation agrees with the single presences of *A. affinis* in the stomach contents of jumbo squid. Shchetinnikov (1986b) reported similar micronektonic squid as prey.

The pelagic red crab substitutes smaller crustaceans in the diet of large jumbo squid. This ontogenetic shift from microplanktonic to macroplanktonic crustaceans has been observed in the diet of other ommastrephids (Rodhouse & Nigmatullin, 1996). The pelagic red crab performs night migrations to the surface, concentrating in dense schools also known to occur in the Gulf of California (Boyd, 1967). Ever larger benthic abundances occur between San Pedro Martir Island and Guaymas (Mathews et al., 1974), which coincides with its presence in the jumbo squid diet.

In contrast to the oceanic relatives of jumbo squid, nerito-pelagic organisms such as anchovy, sardine, and even benthic toadfish, crabs and bottom material are present in their diet. However, the importance of neritic prey has probably been exagerated in the literature (see review in Nesis, 1983; Clarke & Paliza, 2000). A reason may be the relative ease in identifying coastal, more familar fauna than less known mesopelagic nekton, and that myctophids can only be identified through meticulous, time-consuming otolith or bone-based identification. The few works that report the dominance of myctophids in the diet of jumbo squid (Fitch 1976; Shchetinnikov, 1986a,b, 1989) are also those who identified prey in detail.

Cannibalism

Natural explanations have been postulated to explain cannibalism in jumbo squid (Ehrhardt et al., 1983; Clarke & Paliza, 2000). However, cannibalism observed during fishing operations is not evidence that it happens naturally (Hanlon & Messenger, 1996). A few studies have pointed out the possible artificial nature of cannibalism in squid (Breiby & Jobling, 1985; Rodhouse et al., 1992; Seki, 1998). Underwater observations support the idea that cannibalism is induced by jig fishing maneouvres (Bennett, 1978; Bazanov, 1986). There are numerous references documenting attacks on jumbo squid by their conspecific while caught with jigs (Baral, 1967; Nesis, 1983; U. Markaida, personal observation). Jumbo squid remains in stomach contents were identified mostly by the presence of fleshy pieces of 0.5–1 cm^3 (Baral, 1967), that indicate recent ingestion. Moreover, relative prey to predator length is exaggeratedly larger in cases of cannibalism (up to 70–80%) if compared with natural feeding (5–15%) (Bazanov, 1986; Shchetinnikov, 1989; this study). Hanlon & Messenger (1996) stated that cannibalism is intracohortal due to squid schooling behaviour. However, we found that in jumbo squid it is intercohortal, probably due to mixing of schools of different size squid during fishing operations.

Behaviour

The limited observations from this study suggest that jumbo squid feed in surface waters, mostly in the evening or during the first hours of the night, as previously reported (Baral, 1967; Nesis, 1970, 1983; Bazanov, 1986; Shchetinnikov, 1986a,b, 1989; Koronkiewicz, 1988; Ehrhardt, 1991; Clarke & Paliza, 2000). Occasionally, jumbo squid have been seen or caught close to the surface during the day (Roper & Young, 1975). In November 1996, jumbo squid caught off Guaymas were observed feeding on northern anchovy toward the surface in the morning. This behaviour does not seem to be common, although it would explain the occurrence of neritic schooling prey such as anchovy or sardine in the stomach analysed in this study.

Changes in the diet

An ontogenetic transition in diet from planktonic invertebrates to micronektonic fish has been documented (Fitch, 1976; Nesis, 1970, 1983; Shchetinnikov, 1989). Subadult and adult jumbo squid had a well-established diet on myctophids and no ontogenetic changes could be observed in this study, even in smaller squid (20–59 cm ML) (Nesis, 1970). There were no differences among the squid sizes for the main prey, *B. panamense*. Larger variations in diet were observed between different areas or months rather than due to squid sex or size. Geographical and seasonal variations in diet have been previously documented (Shchetinnikov, 1986a; Ehrhardt, 1991).

Ecology

According to fish larval abundance in the Gulf of California, the myctophids *B. panamense* and *T. mexicanus* spawn mainly in June in the deep waters off the western, deep waters coast, compared with the shallower waters of the eastern side (Moser et al., 1974). This distribution pattern coincides with the month and area of the largest jumbo squid catches reported for the 1995–1997 period, and could explain the paradox that jumbo squid concentrate in the western side of the Gulf during summer–autumn although winter and spring upwelling off the eastern coast is stronger (see Markaida & Oscar-Sosa, 2001). Nesis (1970, 1983) identifies the jumbo squid biotope with areas where the primary productivity and zooplankton are relatively high and the number of mesopelagic and bathypelagic fish and macroplankton is maximum. This link reinforces the need to further research on the mesopelagic community of the Gulf of California to understand jumbo squid dynamics.

Adult jumbo squid occupy the niche of medium to large size nektonic predators, which consume organisms of the second and mainly third trophic levels (Nesis, 1970; Shchetinnikov 1986a,b, 1989; this study). According to Chesalin (1994) predation on micronektonic mesopelagic fish by large squid leads to an efficient transfer of energy that supports their unusually high biomass. In annual tropical myctophids, the population is completely replaced every year, and the annual production is as high, or higher than, their standing stock (Gjøsæter, 1981). The same is true for the micronektonic squid that serve as food for jumbo squid. Pelagic red crab live several years, but its consumption shortens the food chain to three trophic levels, increasing the energy efficiency of the ecosystem (Kashkina & Kashkin, 1994). The huge jumbo squid population in the Gulf of California is supported by abundant and efficient resources with high response potential to environmental changes. Dependence on this kind of prey, coupled with the annual life cycle of jumbo squid, might explain the high annual variation in abundance observed in the Gulf of California.

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