Cephalopods from off the Pacific coast of Mexico: biological aspects of the most abundant species*

PILAR SÁNCHEZ

Instituto de Ciencias del Mar, CMIMA-CSIC, Passeig Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.
E-mail pilar@icm.csic.es

SUMMARY: The cephalopod fauna collected in six oceanographic surveys carried out in the northeastern Pacific Ocean off Mexico between March 1990 and June 1992 is analysed. A total of 11 cephalopod species were found at depths of between 16 and 828 m. All the cephalopods were preserved on board and identified in the laboratory. Data on size frequency distribution, and length-weight relationship for the most abundant species (*Dosidicus gigas*, *Lolliguncula diomedae* and *L. panamensis*) are presented. The maturity status of *D. gigas* was also determined in both surveys. Stomach contents revealed that *D. gigas* fed mainly on crustaceans and *D. gigas* itself. The relationship between mantle length and two measurements of the fins of *L. diomedae* and *L. panamensis* and the bathymetric distribution of both species show clear species-specific differences.

Key words: cephalopods, Pacific Ocean off Mexico, *Dosidicus gigas*, *Lolliguncula diomedae*, *Lolliguncula panamensis*.

RESUMEN: CEFALÓPODOS DE LA COSTA PACÍFICA MEXICANA: ASPECTOS BIOLÓGICOS DE LAS ESPECIES MÁS ABUNDANTES. – Se analizó la fauna de cefalópodos que se recogió en seis campañas oceanográficas realizadas en las costas mexicanas del Océano Pacífico nororiental entre marzo de 1990 y junio de 1992. Se encontraron un total de 11 especies de cefalópodos a profundidades entre 16 y 828 m. Todos los cefalópodos se conservaron a bordo y se identificaron en el laboratorio. Se analizaron los datos de frecuencia de tallas y distribución talla-peso de las especies más abundantes (*Dosidicus gigas*, *Lolliguncula diomedae* y *L. panamensis*). Se determinó así mismo, el estado de maduración sexual de *D. gigas* en las dos campañas en las que apareció. Los contenidos estomacales revelan que *D. gigas* se alimenta principalmente de crustáceos así como que canibaliza la propia especie. La relación entre la longitud del manto y dos medidas de las aletas de *L. diomedae* y *L. panamensis* y la distribución batimétrica de ambas especies mostraron una clara diferencia entre especies.

Palabras clave: cefalópodos, Océano Pacífico mexicano, *Dosidicus gigas*, *Lolliguncula diomedae*, *Lolliguncula panamensis*.

INTRODUCTION

The existing bibliography on cephalopods of the waters of the Mexican Pacific is not very extensive and refers mainly to works about octopods (Hochberg, 1980). The teuthofauna of the Central Eastern Pacific Ocean has been revised by Roper *et al.* (1995). Hochberg (1997) made a review of *Octopus rubescens* biology. The technique for trapping the octopus *O. digueti* and reproductive patterns were described by Voight (1988, 1991). The season of reproduction of *O. hubbsorum* was determined in the Bahía de Mazatlán, Sinaloa (Leyva *et al.*, 1987). In the thesis *O. hubbsorum* was misidentified as *O. veligero* (Hochberg personal communication). *Octopus alecto*, *O. chierchiae* and *O. digueti* were recorded for the first time in Bahía de Mazatlán (Mexico) by Mejía-Sarmiento *et al.* (1990). Another

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study in the same area described fishing gear and methods for the capture of octopuses (González-Rendón *et al.*, 1990).

Squids, however, have not been studied as well along the Mexican coast. The species on which most information exists is *Dosidicus gigas*. Papers on this species include studies about fisheries (Hernández-Herrera, *et al.*, 1998; Moral-Bojórquez, *et al.*, 1997; 2001; Nevárez-Martínez *et al.*, 1997; Ehrhardt *et al.*, 1983; Ehrhardt, 1991) and aspects of biology (Ramírez and Klett, 1985; Michel *et al.*, 1986; Ehrhardt *et al.*, 1986; Markaida 2001; Markaida and Sosa-Nishizaki, 2001).

The purpose of this paper is to present observations on cephalopods obtained in 6 surveys carried out during the project "Fundaments for the restructuring of the demersal fisheries of the Mexican Pacific" sponsored by the European Community. The study also presents data on length-weight relationships, size-frequency distributions, maturation and diet of *Dosidicus gigas* and attempts to contribute to establishing the morphological differences between *Lolligunula panamensis* and *L. diomedae*.

MATERIAL AND METHODS

During the research project mentioned above, eight surveys were carried out on board the Mexican oceanographic vessel "El Puma" between March 1990 and June 1992. Species of cephalopods were collected on six surveys.

Two different areas were studied during the project (Fig. 1). The northern sampling area (Sinaloa-Nayarit) covers a 500 km-long portion of continental shelf approximately between latitudes 25°N and 22°N. The main part of the northern study area was situated in the lower Gulf of California. The continental shelf there is relatively wide. Its adjacent coast is an alluvial plain with numerous rivers and large coastal lagoons with permanent inlets, several of which support extensive mangrove forests.

The Southern study area (Oaxaca-Chiapas) was in the Gulf of Tehuantepec. The sampling area was adjacent to 500 km of coastline, between approximately 16°N and 14°N. In its north-western half, which extends to Puerto Angel, the continental shelf is only a few kilometres wide. The south-eastern sector, which extends to Puerto Madero, is characterised by a broad shelf, often in excess of 50 km, which borders a trench 5000 m deep, the deepest in the Eastern Tropical Pacific (Blackburn, 1962).

Three surveys were carried out in the northern area: March 1990 (survey P1), March 1992 (survey P6) and June 1992 (survey P8) and three surveys in the southern area: April 1991 (survey P4), December 1991 (survey P5) and May 1992 (survey P7). A total of 11 cephalopod species were found at depths of between 16 and 950 m. All cephalopods were fixed and preserved on board and later identified in the laboratory. On surveys P2 (June 1990) and P3 (October 1990) the cephalopod species caught were not reported.

FIG. 1. – Study area (Mexican coast, Pacific Ocean) showing the two areas where samples were obtained.

TABLE 1. – List of species found off the Pacific coasts of Mexico. Number of specimens collected during each survey (P1 and P4 to P8) is shown.

	P1	P4	P5	P6	P7	P8
<i>Lolliguncula diomedae</i>	189	5	284	95	127	56
<i>Lolliguncula panamensis</i>		162	16	237	54	68
<i>Abraliopsis falco</i>	4					
<i>Ommastrephes bartramii</i>	12					
<i>Dosidicus gigas</i>	112	51				
<i>Octopus chierchiaie</i>		22			1	
<i>Octopus digueti</i>						1
<i>Octopus hubbsorum</i>					1	
<i>Octopus penicillifer</i>				1		
<i>Octopus rubescens</i>	11				7	1
<i>Argonauta</i> sp	1					

Trawling was carried out using shrimp trawls, with 10.67 m or 24.38 m headrope length, similar to those used by commercial shrimpers in the area. Other nets used included a Mediterranean bottom trawl similar to the one used in Mediterranean fisheries and an Agassiz dredge. Trawl duration varied slightly according to sampling conditions (type of gear and bottom); most tows, however, were in the water for about 30 min. The individuals of *Dosidicus gigas* were caught in two surveys at night, with manual jigging.

During the P1 survey (March 1990) *Dosidicus gigas* was caught in two areas situated at the entrance to the Gulf of California (24°53.5'N, 108°40.2'W and 24°51.2'N, 108°43.1'W) at depths of 215 m and 700 m respectively. In the P4 survey (April 1991) the catches were carried out north of the Gulf of Tehuantepec (18°29.7'N and 104°28.9'W) at a depth of 900 m. Dorsal mantle length (ML) was measured on all specimens and total weight (TW) was recorded. The relationships between ML and TW were calculated using the allometric equation $Y=a \cdot X^b$. The allometric index (b) values were compared by a regression t -test. The sex of all animals was determined and the stage of sexual maturity was recorded. A three-stage maturity scale was used: immature (I), maturing (II) and mature (III). The stomach contents of P1 individuals were also recorded. Stomach fullness was divided into three categories: empty, half-empty and full. The prey was identified to the lowest possible taxonomic level. To quantify diet the following two expressions were used.

(a) The frequency index (Hureau, 1970) was calculated as:

$$F=n_i/Er$$

where n_i = number of prey i present in non-empty stomachs and Er = number of non-empty stomachs.

(b) The numerical importance of each species of prey (R_i) was calculated as:

$$R_i=n_i \cdot 100/N_i$$

where N_i = total number of prey found in the set of non-empty stomachs.

The following measurements of *Lolliguncula diomedae* and *L. panamensis* were recorded: ML, TW, fin length (FL) and fin width (FW). FL, FW and their associated indices (FLI and FWI) were measured according to Roper and Voss (1983): FLI is the greatest length of fins as a percentage of mantle length; FWI is the greatest width (dorsally) across both fins as a percentage of mantle length. To determine the relationship between ML, TW and the two fin measurements, the same methodology as used for the *Dosidicus gigas* ML-TW relationship was used. The bathymetric distribution of both species is also presented.

RESULTS

Eleven species of cephalopods were collected (Table 1) during the sampling period. Six of these species were collected only on one occasion. A small female of genus *Argonauta* without an incubator shell was caught in a haul carried out at a depth of 68 m with a “camaronera” net in the P1 survey. It has been classified as *Argonauta* sp. The sparse material we have available to us makes identification difficult. The small warm-water oceanic squid *Abraliopsis falco* was captured on survey P1 with the Agassiz net.

Length frequencies and some biological data on the most abundant species in the catches.

During the P1 survey a total of 112 individual *Dosidicus gigas* were caught. Of these individuals 13 were males with mantle lengths of between 55 and 73 cm and 99 were females with ML of between

FIG. 2. – *Dosidicus gigas*. Length-frequency distribution for individuals caught during surveys P1 and P4.

66 and 80 cm (Fig. 2). Weights varied from 8 to 17 kg. During the P4 survey 51 individuals were caught (19 males and 32 females). These individuals were smaller than those caught on the previous survey: ML ranged from 15 to 57 cm and weights were 100g and 4 kg. The sex ratio showed a clear predominance of females in both surveys.

ML-TW relationships of *Dosidicus gigas* for every survey were estimated (Table 2). In spite of the differences in size, the comparison of slopes showed a consistent ML-TW relationship between surveys (t-test, $p < 0.1$) as was the case for the ML-

TABLE 2. – *Dosidicus gigas*. Estimated parameters a and b of the mantle length-total weight relationship for males and females caught during surveys P1 and P4. R^2 : correlation coefficient; N: number of individuals.

Survey	Sex	a	b	R^2	N
P1	Males	1.7416	2.048	0.55	7
P1	Females	0.0483	2.919	0.63	43
P1	All	0.0270	3.053	0.80	50
P4	Males	0.0213	3.052	0.99	23
P4	Females	0.0196	3.102	0.99	19
P4	All	0.0210	3.066	0.99	42
P1+P4	Males	0.0178	3.111	0.99	30
P1+P4	Females	0.0132	3.221	0.99	62

FIG. 3. – *Dosidicus gigas*. Percentage of males and females at each maturity stage during surveys P1 and P4.

TW relationships for males and females calculated separately.

As a result, the data were combined for both surveys. In this case the comparison of slopes did not provide evidence for significant differences between sexes (t-test, $p < 0.07$).

Figure 3 shows the relative frequency of the different stages of sexual maturity amongst the individual *Dosidicus gigas* caught. In survey P1 (March) 85% of the males were fully mature, whereas in contrast only 65% of the females were mature. In survey

TABLE 3. – *Dosidicus gigas*. Dietary composition. Data presented are: %: percentage contribution to the diet; F : frequency index; R_i : index of numerical importance.

	%	F	R_i
CRUSTACEA	62.86		
<i>Pleuroncodes planipes</i>		0.617	52.857
<i>Penaeus</i> spp		0.117	10.000
MOLLUSCA	31.43		
Loliginidae		0.050	4.286
<i>Dosidicus gigas</i>		0.317	27.143
PISCES	5.71		
Myctophidae		0.033	2.857
<i>Diaphusteta</i> sp		0.017	1.429
Unidentified		0.017	1.429

P4 (April) 56% of the males and 63% of the females were mature respectively, somewhat less than in the previous survey. As mentioned above, although they were somewhat smaller in size, the percentage of mature squid is fairly high.

As regards feeding, studies made from the individual *Dosidicus gigas* caught in the P1 survey, the pelagic red crab (*Pleuroncodes planipes*) found in large quantities in the area, was the most abundant prey in the stomach contents (Table 3). The next

most abundant prey was *D. gigas*, which indicates that cannibalism exists between the large animals. The remains of others crustaceans, loliginids and fishes (mainly Myctophidae) were also observed.

Sizes of *Lolliguncula diomedae* captured ranged between 29 and 77 mm ML for males and between 38 and 103 mm ML for females (Fig. 4). In the P5 and P6 surveys carried out in December 1991 in the southern area, and in March 1992 in the northern area respectively, small animals were absent.

FIG. 4. — *Lolliguncula diomedae*. Distribution of length frequencies for each survey.

TABLE 4. – *Lolliguncula diomedeeae*. Estimated parameters a and b of relationship $Y = a \cdot X^b$. ML: mantle length (mm), TW: total weight (g), FL: Fin length, FW: Fin width, r^2 : correlation coefficient, N : number of individuals.

	Sex	a	b	r^2	N
ML vs. TW	Males	0.0001	2.948	0.95	16
ML vs. TW	Females	0.0020	2.013	0.85	34
ML vs. TW	All	0.0011	2.169	0.92	50
ML vs. FL	Males	0.0730	1.396	0.89	16
ML vs. FL	Females	0.1009	1.301	0.90	34
ML vs. FL	All	0.1197	1.262	0.96	50
ML vs. FW	Males	0.1077	1.384	0.79	16
ML vs. FW	Females	0.1284	1.290	0.86	34
ML vs. FW	All	0.3911	1.033	0.88	50

FIG. 5. – *Lolliguncula diomedeeae* and *Lolliguncula panamensis*. Fin length-mantle length relationship.

FIG. 6. – *Lolliguncula diomedeeae* and *Lolliguncula panamensis*. Fin width-mantle length relationship.

Considering the high growth rates of cephalopods, this suggests that spawning takes place in winter, with the first juveniles being caught in spring. In all the surveys, female *L. diomedeeae* were more numerous than the males, from 70.1% in the P8 survey to 82.1% in the P7 survey.

Table 4 shows the estimated parameters of the ML-TW, FL-ML and FW-ML relationships for both male and female *Lolliguncula diomedeeae* and the overall population (males + females) (see also Figs. 5 and 6). A comparison between the estimated parameters for males and females showed that growth pattern differed significantly between the sexes (t-test, $p < 0.01$). The values for the indices FLI and FWI (mean and range) were 35.3 (25.3-40.4) and 44.9 (30.9-53.9) respectively. *L. diomedeeae* was captured at depths of between 25 and 190.5 m (Fig. 7) with 90% of all individuals taken at depths greater than 45 m.

The sizes of *Lolliguncula panamensis* caught varied between 25 and 83 mm ML for males and between 27 and 106 mm for females (Fig. 8). In the P6 (March 1992, northern area) and P7 (May 1992, southern area) surveys the presence of juveniles was of special importance. The proportion of females ranged from 48.1% in the P7 survey to 94.1% in the P8 survey.

Table 5 shows the estimated parameters of the ML-TW, FL-ML and FW-ML relationships for both

FIG. 7. – *Lolliguncula diomedeeae* and *Lolliguncula panamensis*. Abundance distribution by depth.

TABLE 5. – *Lolliguncula panamensis*. Estimated parameters a and b of relationship $Y = a \cdot X^b$. ML: mantle length (mm), TW: total weight (g), FL: Fin length, FW: Fin width, r^2 : correlation coefficient, N : Number of individuals.

	Sex	a	b	r^2	N
ML vs. TW	Males	0.0002	2.67	0.98	33
ML vs. TW	Females	0.0001	2.809	0.99	55
ML vs. TW	All	0.0002	2.741	0.98	88
ML vs. FL	Males	0.2961	1.141	0.96	33
ML vs. FL	Females	0.3113	1.131	0.98	55
ML vs. FL	All	0.2992	1.140	0.98	88
ML vs. FW	Males	0.8059	0.933	0.92	33
ML vs. FW	Females	0.4963	1.063	0.96	55
ML vs. FW	All	0.5710	1.037	0.95	88

FIG. 8. – *Lolliguncula panamensis*. Distribution of length frequencies for each survey.

male and female *Lolliguncula panamensis* and for the overall population (males + females) (see Figs. 5 and 6). A comparison between the estimated parameters for males and females showed that growth pattern differed significantly between the sexes (t-test, $p < 0.01$), although the differences between sexes are less marked than in *L. diomedae*. The values for the indices FLI and FWI (mean and range)

were 51.7 (42.6-60.4) and 63.4 (52.0-75.9) respectively. *L. panamensis* was captured at depths of between 16 and 65.5 m (Fig. 7). 90% of all individuals were taken at depths of less than 45 m.

Comparing results for the two *Lolliguncula* species, it may be seen that the fin of *L. diomedae* is shorter and narrower than that of *L. panamensis*, as confirmed by the differences in FLI and FWI val-

ues. The ML-TW relationships reveal that *L. diomedae* has a “thinner”, more fusiform, body than *L. panamensis* (Tables 4 and 5).

DISCUSSION

In Panama, *Loliguncula panamensis* and *L. diomedae* are taken as by-catch in the commercial shrimp fishery (Roper *et al.*, 1995). Usually the squid are discarded and only a small number of samples reach the local market, as also seems to happen in Mexico. In spite of their small size these species could be exploited commercially. *Abraliopsis falco* lives in warm oceanic waters and was described by Young (1972) from samples captured in the north-eastern Pacific Ocean between Baja California and Isla Guadalupe. Due to its small size it is unusual for it to be caught with commercial nets of a big mesh size.

Some authors (Nesis, 1983; Nigmatullin *et al.*, 2001) have pointed out the possibility of three populations of *Dosidicus gigas* in the Pacific Ocean. The first consists of small individuals that mature early in the near equatorial area. The second, and most numerous, comprises intermediate sized individuals that mature late and live within the whole species range (except at the highest latitudes) and a third population, occurring at the northern and southern peripheries of the range, has large individuals that also mature late. According to this hypothesis the individuals captured in the P1 survey would belong to a third group, while those captured in the P4 survey would belong to the firsts group. On the other hand, Clarke and Paliza (2000), after reviewing the horizontal distribution of *D. gigas*, concluded that the populations in the northern and southern hemispheres are distinct, possibly different subspecies. Nigmatullin *et al.* (2001) pointed out that the different groups are in fact well separated from each other and represent species *in status nascendi*, or at least different population systems (or stock units). This suggests the need for a more detailed analysis of population structure of the species.

Ehrhardt *et al.* (1983) reported that during most of the year mature female *Dosidicus gigas* are found in some abundance. The high percentage of fully mature females in December-January and May-June indicates that there are two main spawning seasons during the year. Markaida and Sosa-Nishizaki (2001) found, in the Gulf of California, mature females in all months although they rarely exceeded

25% of the total, implying a reproductive cycle throughout the year with no particular peak.

Ehrhardt (1991), in his analysis of the stomach contents in samples of *Dosidicus gigas* collected in January to September, found a high degree of cannibalism (higher in March) and very high predation on sardines (*Sardinops sagax caerulea*), especially in May to September. He indicated that the later predation would affect the fishery for sardines. Markaida (2001) reported that the diet of *D. gigas* was dominated by *Benthosema panamense*, an abundant nyctoepipelagic myctophid, and to a lesser degree by *Triphoturus mexicanus*. Secondary prey was important in some months, in particular mesopelagic cephalopods, pelagic red crab (*Pleuroncodes planipes*) and small pelagic fishes such as northern anchovy (*Engraulis mordax*) or Pacific sardine (*Sardinops sagax*). The aggressive character of *D. gigas* became apparent in the catches: on some occasions it was possible to observe animals of the same species attacking animals caught by the jigs (Wormuth, 1971; Nesis, 1983; Ehrhardt *et al.*, 1983; this study). The incidence of cannibalism increases with size. Some authors have pointed out that the cannibalism is a consequence of the use of squid as bait during fishing activities (Bazarov, 1986; Markaida, 2001).

A recent review of the family Loliginidae (Vecchione *et al.*, 1998) reclassified many species of this family. All species in the genus *Loliguncula* are united and distinguished from other loliginids by the long cement body of their spermatophores. There exists variability in hectocotylus morphology. This is extreme in *L. diomedae* but Brakoniecky (1986) has pointed out the similarities in hectocotylisation between this species and the others of *Loliguncula*.

Brakoniecki (1980) differentiated *L. panamensis* from *L. tydeus* based on the relative length of the hectocotylised arm, which in *L. tydeus* is about equal in length to its fellow arm. Because no male *L. panamensis* was seen, *L. brevis* (from the western Atlantic Ocean) was used for comparison because it is morphologically nearly identical to *L. panamensis*. Later Brakoniecki (1986) considered *L. tydeus* to be conspecific with *L. panamensis*, of which previously he had seen only females.

This study has allowed us to clarify and extend the systematic description of *Loliguncula diomedae* and *L. panamensis*. Males of *L. diomedae* have two modified ventral arms, the left of which is proportionally longer (76-107% ML) than that of *L. panamensis* (42-69% ML).

Given that the descriptions of the species are based on the morphological characteristics of the males, we have tried to differentiate the two species by other features that are common to both males and females. The characteristics that we found to be the most obvious were the length and width of fins (Figs. 5 and 6). The fin of *L. diomedae* is shorter and narrower than that of *L. panamensis*. The indices of these measurements confirm these differences.

In addition, the ML-TW relationships of the species *Lolliguncula panamensis* and *L. diomedae* show clear differences between them: *L. diomedae* is "thinner" than *L. panamensis*, that is to say, its body has a more fusiform shape (Tables 4 and 5). There is also a marked difference between the females and the males of *L. diomedae*, a difference that is not noticeable in *L. panamensis*.

Another important difference between the two species is their bathymetric distribution. *L. panamensis* principally inhabits depths of less than 45 m, whereas *L. diomedae* shows a much wider depth range, although with high abundance between 45 to 200 m (Fig. 7). Barrientos (1987) caught *L. panamensis* between 12 to 120 m depth but most were taken between 12 and 70 m. This author pointed out that he rarely found *L. panamensis* and *L. diomedae* in the same trawl and suggested that it could be the result of competitive exclusion.

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