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Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria lucetia*) in the Humboldt Current System off Peru

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SUMMARY: Acoustic surveys for assessing the biomass and distribution of the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria lucetia*) were carried out in the Humboldt Current System of Peru in 2007 and 2008. At the same time, 937 jumbo squid were caught and their stomach contents analyzed. The diet of the jumbo squid was dominated by mesopelagic fish. The first component of their fish diet was *V. lucetia* and the second component was the myctophid fish *Diogenichthys laternatus*. Acoustic biomass estimates of these species show that *V. lucetia* is an important component in aggregative structures in the Humboldt Current System of Peru and its distribution and movements are closely related to the migratory movements of the jumbo squid. The trophic relationship observed between *D. gigas* and *V. lucetia* promotes an increase in jumbo squid biomass and, has a positive trophic effect on the ocean ecosystem.

Keywords: jumbo squid, *Dosidicus gigas*, *Vinciguerria lucetia*, trophic relationships, acoustic method, Humboldt Current.

RESUMEN: Relaciones tróficas entre el calamar gigante *Dosidicus gigas* y el pez luminoso *Vinciguerria lucetia* en el sistema de la corriente de Humboldt de Perú. – La biomasa de calamar gigante *Dosidicus gigas* y el pez mesopelágico *Vinciguerria lucetia* se obtuvo a partir de detección acústica en la Corriente de Humboldt de Perú durante 2007 y 2008. Simultáneamente, 937 calamares fueron capturados y se les analizó el contenido estomacal. La dieta de *D. gigas* estuvo dominada por peces, siendo *V. lucetia* el principal componente y en segundo lugar el mictófido *Diogenichthys laturnatus*. A partir de la evaluación de la biomasa de ambas especies, estimada por el método acústico, se observó que *V. lucetia* es uno de los principales componentes en el sistema de la Corriente de Humboldt de Perú y sus patrones de distribución y movimientos espacio-temporal están fuertemente relacionados a los desplazamientos migratorios del calamar. Estas relaciones tróficas promueven un incremento de la biomasa de *D. gigas* que es resultado de un patrón similar en *V. lucetia*, lo que propicia un efecto trófico positivo en el ecosistema oceánico.

Palabras clave: calamar gigante, *Dosidicus gigas*, *Vinciguerria lucetia*, relaciones tróficas, método acústico, corriente de Humboldt.

INTRODUCTION

The jumbo squid *Dosidicus gigas* (d`Orbigny, 1835) is a voracious predator that attacks a great variety of prey, including fish, crustaceans and other invertebrates (Ehrhardt *et al.,* 1986, Markaida and Sosa-Nishizaki, 2003, Markaida *et al.,* 2008). It is considered an important organism in the ecosystem due to its voracity and its tendency not to feed selectively (Markaida and Sosa-Nishizaki, 2003). It has become an important commercial resource in the eastern Pacific Ocean. In Peru the jumbo squid fishery has been one of the most important fisheries since 1990 (Yamashiro *et al.,* 1998, Markaida and Sosa-Nishizaki, 2003, Rosas-Luis *et al.,* 2008, Keyl *et al.,* 2008). This species feeds mainly at night, but there are reports of jumbo squid feeding during the day in the California Current System of Mexico (Markaida and Sosa-Nishizaki, 2003, Rosas-Luis *et al.,* 2008), and in the Humboldt Current System of Peru (Alegre-Norza, personal observations, 2010), which shows that the species carries out both vertical (Gilly *et al.,* 2006) and horizontal migrations (Markaida *et al.,* 2005).

In the Humboldt Current System of Peru, upwelling events on the coast result in high concentrations of primary and secondary production that are exploited by *D. gigas* and other species such as mesopelagic fish. A remarkable feature of mesopelagic fish, such as the lanternfish (Myctophidae) and lightfish (Phosichthyidae), is that they perform extensive vertical migrations and form dense patches. Vertical migration is one of the most widespread patterns of animal behaviour in mesopelagic zones (Frank and Widder, 2002), and influences the life histories of non-migrating and migrating fish and cephalopods (mainly the jumbo squid) and the feeding behaviour and spatial distribution patterns of predators (Konchina, 1983, Benoit-Bird and Au, 2002, Bertrand *et al.,* 2002). Aggregations, densities and the geographic distribution of species can be quantified and mapped by acoustic methods, such as sound scattering layers (Lapko and Ivanov, 1994, Luo *et al.,* 2000, Cornejo and Koppelmann, 2006). This is very useful for estimating the abundance of marine organisms. Data from acoustic surveys can also provide biological information, such as spatial distribution patterns and migratory movements. These methods have therefore been used to study the predator-prey relationship when species are well discriminated (Miyashita *et al.,* 2004). For *D. gigas*, the acoustic method has been standardized and acoustic detection has frequently been used to estimate biomass in Mexico and Peru (Benoit-Bird *et al.,* 2008). However, acoustic detection of the lightfish (*Vinciguerria lucetia,*Garman, 1899) is always compared with trawls that are monitored and controlled by an acoustic net-recorder (Marchal and Lebourges, 1996, Cornejo and Koppelmann, 2006).

Dosidicus gigas is an important commercial resource and like *V. lucetia,* it is important to marine ecology. *V. lucetia* is one of the most abundant species of mesopelagic fish in the eastern Pacific Ocean both in tropical and warm waters (Ahlstrom, 1968), and it has been reported in studies on the feeding habits of squid (Schetinnikov, 1986, Schetinnikov, 1989, Markaida and Sosa-Nishizaqui, 2003, Markaida, 2006, Rosas-Luis, 2007). Due to the abundance of *D gigas*, its feeding behavior and its importance as a fishery resource, and also the dynamism and abundance of *V. lucetia*, the objective of this study was to determine the trophic relationship between *D. gigas* and *V. lucetia* in the pelagic ecosystem in the southeast Pacific Ocean off Peru (Fig. 1), based on the data analysis of acoustic measurements, midwater trawl fishing and stomach content analyses in 2007 and 2008.

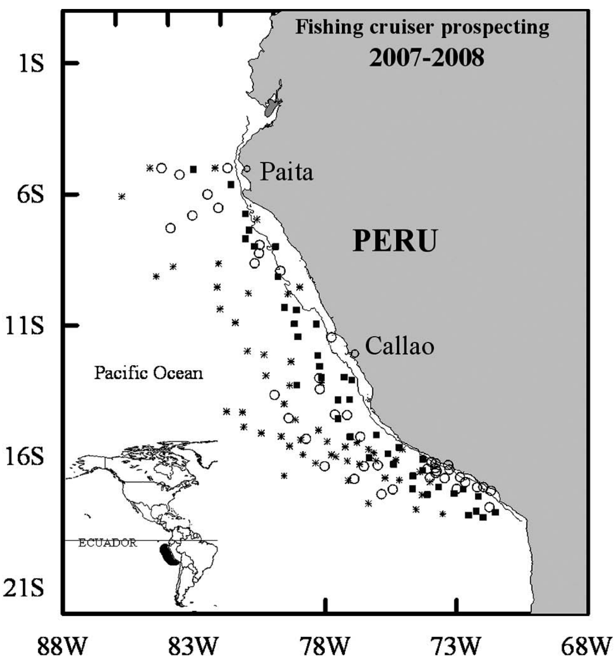

FIG. 1. – Pacific Ocean off Peru, principal area of jumbo squid fishing in the Humboldt Current System (Fishing cruiser prospecting: ■.March 2007, *June-July 2008 and, ○ November-December 2008).

MATERIALS AND METHODS

Biological data

Three bio-acoustic surveys were carried out by the Instituto del Mar del Peru (IMARPE) aboard the BIC *Humboldt* and *José Olaya Balandra* in the Humbold Current System off Peru in March (summer) of 2007 and June-July (autumn-winter) and November-December (spring) of 2008.

Jumbo squid were caught, measured and the stomach contents were sampled. Hard structures and tissues of fish, cephalopods and crustaceans were used to identify prey in 829 stomach, while 108 stomachs were empty. The stomach contents were passed through a 500 μ mesh sieve in the Trophic Ecology Laboratory of IMARPE. Observations were made under a binocular microscope (60-120x) over a black and white background to aid identification.

Hard structures were identified by consulting the work of Fitch and Brownell (1968), and Garcia-Godos (2001) for fish, Wolff (1984) for cephalopods, Newel (1963) and Mendez (1981) for crustaceans and Alamo and Valdivieso (1987) for molluscs.

Frequency of occurrence and numeric and gravimetric methods were used to quantify the diet. The

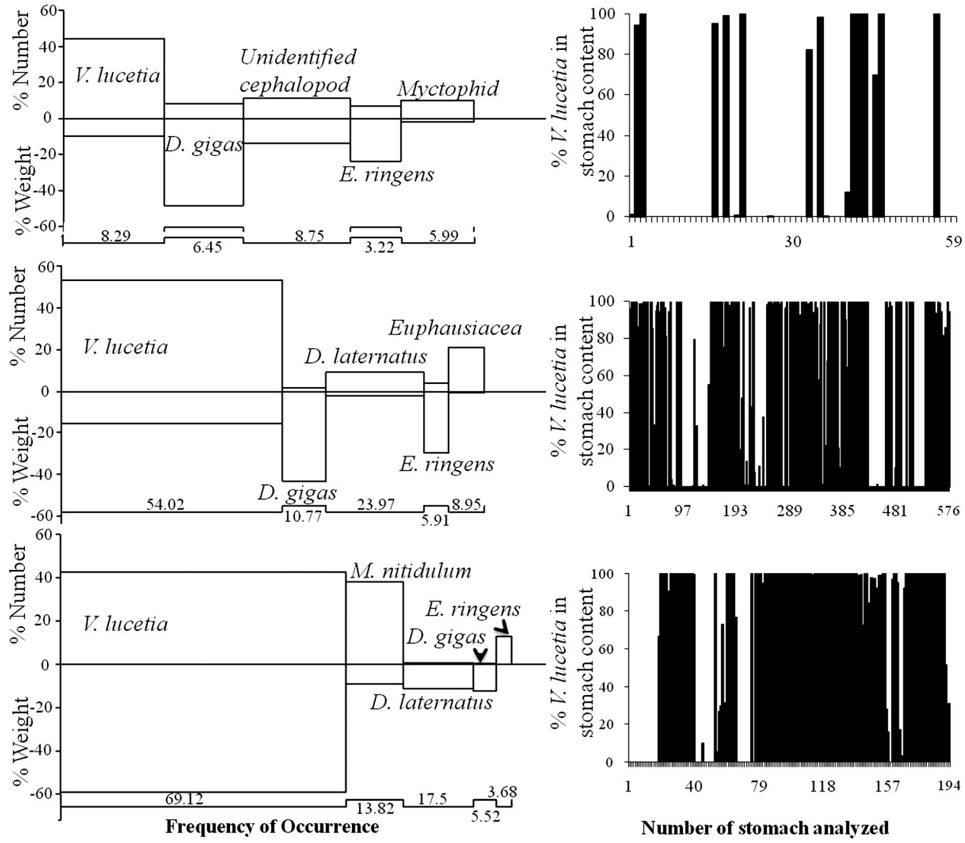

Fig. 2. – Left: Composition by percentage number (%N) and weight (%W)(vertical axis) and frequency of occurrence (%FO, horizontal axis) of the main prey found in the stomach contents of jumbo squid collected in the Humboldt Current System off Peru (March 2007, June-July 2008 and November-December 2008). Right: Percentage of *V. lucetia* found in the stomach contents of jumbo squid.

frequency of occurrence (%FO) was calculated as the percentage of jumbo squid that fed on a certain prey, the number (%N) was the number of individuals of a certain prey in relation to the total number of individual prey, and the weight (%W) was defined as the weight of a certain prey in relation to the total weight of all the prey (Cailliet, 1977).

Graphs of the index of relative importance (IRI) were plotted to illustrate the diet compositions obtained from scientific cruises (Pinkas *et al.,* 1971) (Fig. 2). The most important prey according to the IRI were included in the plots. IRI= (%N+%W)*%FO.

Acoustic data

Acoustic data were collected with a Simrad EK60 dual frequency quantitative scientific echo sounder that consisted of split-beam transducers of 38 and 120 kHz mounted on the ship's hull, which were calibrated prior to the survey using standard procedures (Foote *et al.,* 1987). The data were processed with Echoview (Simmonds and MacLennan, 2005). The water column was investigated down to depths of 500 m. Figure 3 shows the acoustic survey area and the 11 parallel transect lines. Each transect line crossed the continental shelf to the oceanic zones (about 300 nautical miles from the shore), where sea depths range from 5 to 500 m. A daytime survey (from 1 h after sunrise to 1 h before sunset) and a night-time survey (from 1 h after sunset to 1 h before sunrise) were conducted for each transect line within 24 h.

For mesopelagic fish, acoustic detection with a -70 dB threshold was applied to minimize bias due to noise or non-mesopelagic fish. With this threshold, the nautical-area-backscattering coefficients were recorded along survey tracks at georeferenced elementary distance sampling units of 1 nautical mile each. The result can be considered to represent the biomass of mesopelagic fish (Bertrand *et al.,* 1999, MacLennan *et al.,* 2002). Sometimes several species were found in mixed concentrations so that the marks on the echogram from each species could not be distinguished. The echogram shows that the echo-integrals can provide data about a group of mixed species as one category, but not about the individual species. However, it is possible to make further divisions to species level by referencing the composition of the trawl catches (Nakken and Dommasnes, 1975). To support this process, organism samples were collected at the same time by non-closing pelagic trawls (Length: 55 m: mesh codend: 13 mm). Commercial midwater trawls were used to determine the taxonomic composition of the mesopelagic fish in

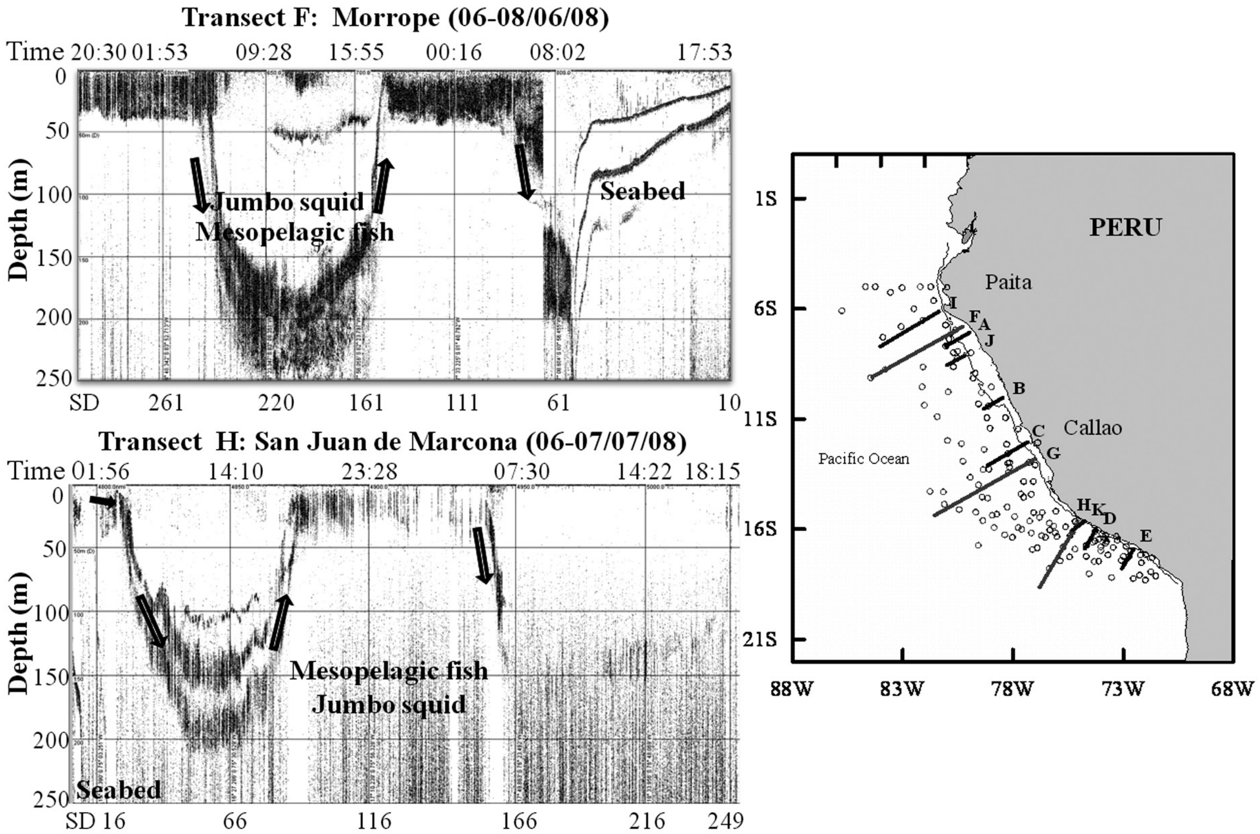

FIG. 3. – Acoustic detection of *V. lucetia* and *D. gigas* in 2007 and 2008 in the Humboldt Current System off Peru. Transect A, B, C, D and E were completed in March 2007; F, G and H in June-July 2008; and I, J and K in November-December 2008. SD, seashore distance in nautical miles. Vertical movements of jumbo squid and *V. lucetia* were clearly detected in the echogram of transects F and H.

the water column according to the distribution of the sound scattering layers (SSLs) observed on the echo sounder. Acoustic backscatter energy was detected in up to four layers of 50 m intervals (5 to 220 m) during the night-time and up to ten layers (5-500 m) during the daytime.

The nautical-area-backscattering coefficients (S_A) were calculated for each trawl for cells in which fish were present (S_A+), which is an index of fish density. We used the following expression for calculating the biomass:

$$Biomass = C \cdot A <S_A>$$
$$C = C_i/(1000\ \sigma_{kg})$$
$$\sigma_{kg} = 4\pi\ 10^{TSkg/10}$$
$$TS_{kg} = TS - 10\ log\ (<w>/1000)$$

V. lucetia: TS= 20 Log L-79.06 (dB), L: 3.5 to 6.5 cm (Gutierrez and Herrera, 1998)
D. gigas: TS= 20 Log L-92.82 (dB), L: 65.5 to 93.5 cm (Castillo and Gonzales, 2000)
D. gigas: TS= 20 Log L-86.17 (dB), L: 22 to 38 cm (Castillo and Gonzales, 2000)

where:
TS: target strength, specific to each species.
$<S_A>$: nautical coefficient average of dispersal area (m^2/nm), ecointegration average of isoparalitoral area.
A: isoparalitoral area (nm^2)
σ_{kg} : retrodispersed acoustic section (kg).
C_i: instrumental constant of echosounder.
$<w>$: weight average of species (g).
L: body length of a scatterer (normally this is the total length for fish, and dorsal mantle length for squid)
C: acoustic constant.

Consumption of *V. lucetia*

The percentage of *V. lucetia* in the total stomach contents of each jumbo squid was calculated and plotted to show the trophic relationship between these two species. To estimate the consumption rate (Q*i*) of *V. lucetia* by *D. gigas*, we determined three parameters: (1) the biomass of the predator (B*j*); (2) the consumption-biomass relationship of the predator (Q/B)*j* [taken from Alarcon-Muñoz *et al.* (2008)]; and (3) the diet composition (DC*ij*) of the prey (*i*) in the stomach contents of the predator (*j*). The following expression was used to calculate the consumption rate:

$$Q_i = \sum_{i=1}^{n} B_j \left(Q / B\right)_j \cdot DC_{ij}$$

Table 1. – Summary data of jumbo squid collected in the Humboldt Current system off Peru in 2007-2008

Fishing cruiser prospecting	Date	Female	Sex Male	Unknown	Total	Mantle length (cm)
Bic. Olaya 0702-04	March 3-10	30	29	2	61	14.5-81.5
Bic. Humboldt 0805-07	June 4-July 12	346	313		659	6.7-103.5
Bic. Humboldt 0811-12	November 9- December 18	96	114	7	217	3.2-101.0
Total		472	456	9	937	3.2-103.5

RESULTS

A total of 937 jumbo squid was sampled (472 females, 456 males and 9 unknown). The dorsal mantle length (ML) was measured, and ranged in size between 3.2 and 103.5 cm (Table 1). The most usual size of males and females was 10 to 30 cm ML, and large jumbo squid (>70 cm ML) were observed on all research cruises.

Diet description

The stomach contents of *D. gigas* revealed two main groups: fish and molluscs (mainly cephalopods). Fish were found in practically every stomach (81.62% FO) in 2008 and (18% FO) 2007, and were the most important group in both years. The index of relative importance (IRI) was used to determine the importance of each group in the diet of *D. gigas*. In 2007 fish and cephalopods (Teuthida) were the most important groups and we observed that *D. gigas* fed primarily on these two groups (Fish IRI=1841, Teuthida=1238). The situation changed drastically in 2008, when jumbo squid were found to feed mainly on fish (Fish IRI=12795.82 and Teuthida=852.5). *V. lucetia* was the main item in the jumbo squid diet. In 2007 it accounted for 44.1%N, IRI=445.4, and in 2008 it was present in over half of the samples (54% and 69.12% FO) and accounted for 53.3% and 42.6%N (IRI=3734 and 7029). The second most important fish was the myctophid *Myctophum nitidulum*, which was present in both years, and showed particularly high values in November-December 2008 (IRI=651). Another myctophid in the squid's diet was *Diogenichthys laternatus*, which was only present in 2008 (IRI 268 and 199) (Table 2).

Cephalopods were next in importance, and were found in 19.4% of stomachs in 2007 and 10.8%, and 5.53% in 2008, and accounted for 19.4% of the prey in 2007 and 4.62% and 0.77% in 2008. *D. gigas* was the main item in the group as it was found in 6.45% of samples in 2007 and accounted for 8.24% of prey (IRI= 364.3). In 2008 its importance in the diet declined (IRI=479.7 and 69.7)(Table 2).

Other groups were present in the diet such as the crustaceans: *Pleuroncodes monodon*, pteropoda and protista but they were not significant (IRI less than 35) (Table 2).

The stomach samples collected represent the climatic seasons of Peru: March (summer), June-July (autumn-winter) and November-December (spring). *D. gigas* mainly fed on *V. lucetia* in the three seasons (Fig. 2), and the importance of this fish increased throughout the year (IRI summer= 445.4, autumn-winter= 3734 and spring= 7029.2) (Fig. 2, spelling bars). The diet of *D. gigas* did not vary over the year, and we always found the same prey groups (fish, cephalopods and crustaceans); however, the frequency of occurrence of these groups varied in the two years (Table 2).

Acoustic observation of the distribution patterns of *D. gigas* and *V. lucetia*

Typical echograms at 38 and 120 kHz (Fig. 3) allowed us to explain the distribution patterns and the aggregative behaviour of *D. gigas* and *V. lucetia* in the Humboldt Current System of Peru. We observed the daily vertical migration of mesopelagic fish distributed in the sound scattering layers. The midwater trawls indicated that these acoustic structures were formed mainly by micro-nektonic organisms such as *V. lucetia*. In the summer 2007, *D. gigas* was detected at depths of between 2 and 215 m, and it was observed interacting with *V. lucetia* (Fig. 3). The distribution of the two species was similar at between 26 and 290 nautical miles (nm) from the seashore. Both species came close to the surface water at night, and migrated to deeper waters during the day. Biomass detection of these species with acoustic methods showed *V. lucetia* to be a principal component of the mesopelagic system, and its movements were related to those of *D. gigas*.

Transect F and H in Figure 3 show important interaction between *D. gigas* and *V. lucetia* in 2007 and 2008. The echograms were plotted during day and night. The vertical migration of the two species is the main component of the echogram; during the day, they occupied deeper waters from 120 to 300 m depth and at sunset they returned to surface water. Generally, *D. gigas* and *V. lucetia* shared the same distribution range at the same times. In the northern area at night they were detected in two areas (257-300 nm and 60-160 nm) near the surface water and at 50 m depth, whereas in the day the distribution was between 160 and 250 nm in deeper water (155-250 m depth) (Transect F). The same day-night pattern was found in the southern area, but the distribution of the two species was between 20 and 160 nm (Transect H).

Consumption of *V. lucetia* by *D. gigas*

Table 3 shows the acoustic biomass estimates of *D. gigas* and *V. lucetia* obtained in 2007 and 2008. Ac-

TABLE 2. – Frequency of occurrence (FO), number (N), and weight (W) of prey in the stomach contents of jumbo squid during 2007-08, weight in grams.

	March 3-10, 2007							June 4-July 12, 2008							November 9-December 18, 20						
	FO	FO%	N	N%	W	W%	IRI	FO	FO%	N	N%	W	W%	IRI	FO	FO%	N	N%	W	W%	IRI
Pices																					
Mycthophidae	39	17.97	111	65.3	125	37.11	1840.50	529	80.27	3184	71.40	2524.52	55.24	10165.65	180	82.95	7498	98.52	2462.45	87.43	15426
Myctophum aurolaternatum								21	3.19	29	0.65	99.87	2.19	9.04	10	4.61	21	0.28	13.43	0.48	3.5
Myctophum nitidulum	2	0.92	2	1.18	1.79	0.53	1.57	11	1.67	13	0.29	7.75	0.17	0.77	30	13.82	2897	38.07	253.97	9.02	651
Diogenichthys laternatus								158	23.98	400	8.97	101.24	2.22	268.15	37	17.05	44	0.58	313.71	11.14	199.80
Lampanyctus sp.								30	4.55	38	0.85	12.21	0.27	5.10	5	2.30	10	0.13	130.95	4.65	11
Myctophum sp.								5	0.76	24	0.54	18.30	0.40	0.71	5	2.30	27	0.35	16.70	0.59	2.20
Unidentified Myctophidae	13	5.99	17	10	6.70	1.98	71.79	30	4.55	61	1.37	23.73	0.52	8.59	5	2.30	155	2.04	28.46	1.01	7
Phosichthydae																					
Vinciguerria lucetia	18	8.29	75	44.12	32.35	9.58	**445.39**	356	54.02	2379	53.34	720.74	15.77	**3733.62**	150	69.12	3239	42.56	1665.17	59.13	**7029.20**
Bathylagidae																					
Leuroglossus sp.								4	0.61	5	0.11	2.09	<.05	0.10							
Carangidae																					
Trachurus murphyi								1	0.15	1	<.05	22.03	0.48	0.08							
Nomeidae																					
Cubiceps pauciradiatus								13	1.97	14	0.31	144.10	3.15	6.84	6	2.76	125	1.64	38.25	1.36	8.29
Engraulidae																					
Engraulis ringens	7	3.23	12	7.06	79.78	23.61	98.95	39	5.92	172	3.86	1356.35	29.68	198.49	8	3.69	980	12.88	1.80	0.06	47.71
Unidentified fish	5	2.30	5	2.94	4.77	1.41	10.03	40	6.07	48	1.08	16.12	0.35	8.67							
Teuthida	33	15.21	33	19.41	209.44	61.99	1237.97	198	30.04	206	4.61	200.74	43.78	1454.33	41	18.89	59	0.77	351.92	12.49	250.74
Ommastrephidae																					
Dosidicus gigas	14	6.45	14	8.24	162.95	48.23	364.29	71	10.77	72	1.61	1960.79	42.91	479.71	12	5.52	29	0.38	344.46	12.23	69.74
Enoploteuthidae																					
Abraliopsis affinis								88	13.35	96	2.15	30.59	0.67	37.68	19	8.76	21	0.28	5.16	0.18	4.01
Unidentified teuthida	19	8.75	19	11.18	46.50	13.76	218.38	38	5.77	38	0.85	9.36	0.20	6.09	9	4.15	9	0.12	2.31	0.08	0.83
Crustacea																					
Euphausiacea	2	0.92	14	8.24	0.55	0.16	7.74	59	8.95	936	20.99	36.93	0.81	195.13							
Galatheidae																					
Pleuroncodes monodon	8	3.69	11	6.47	2.46	0.73	26.54														
Ostracoda								11	1.67	44	0.99	0.32	<.05	1.66							
Cancridae paralarvae								1	0.15	1	0.02	0.06	<.05	<.01	1	0.46	24	0.32	<.05	<.05	<.05
Unidentified crustacea								8	1.21	8	0.18	1.12	<.05	0.25							
Pteropoda																					
Atlanta sp.	1	0.46	1	0.59	<.05	<.05	0.27	14	2.12	20	0.45	<.05	<.05	0.95	1	0.46	5	0.07	<.05	<.05	<.05
Diacria sp.								7	1.06	17	0.38	0.40	<.05	0.41	9	4.15	9	0.12	1.78	0.06	0.75
Unidentified								7	1.06	39	0.87	2.30	0.05	0.98	1	0.46	13	0.17	0.09	<.01	0.08
Gastropoda																					
Natica sp.								4	0.61	4	0.09	<.01	<.01	0.05	4	1.84	2	<.01	<.05	<.05	<.05
Protista																					
Phaeophyceae																					
Laminariales								1	0.15	1	0.02	3.01	0.07	<.01							
Total			170		337.85					4460		4569.43					7610		2816.27		

TABLE 3. – Acoustic biomass estimation of jumbo squid and *V. lucetia*, and estimated consumption of *V. lucetia* by *D. gigas* between 2007 and 2008. Q/B of jumbo squid= 5.8, taken from Alarcon-Muñoz *et al.* (2008).

Fishing cruiser prospecting	*DCij*	Hydroacoustic biomass *D. gigas* (t)	*D. gigas* predation on *V. lucetia* (t)	Hydroacoustic biomass *V. lucetia* (t)	Estimation of predation by jumbo squid on *V. lucetia* biomass %
2007 02-04	0.09	1231713.3	625390.1	5948499.9	10.51
2008 05-07	0.15	717086.8	570084.0	2445635.2	23.31
2008 11-12	0.59	154047.0	481704.9	8317821.4	5.79

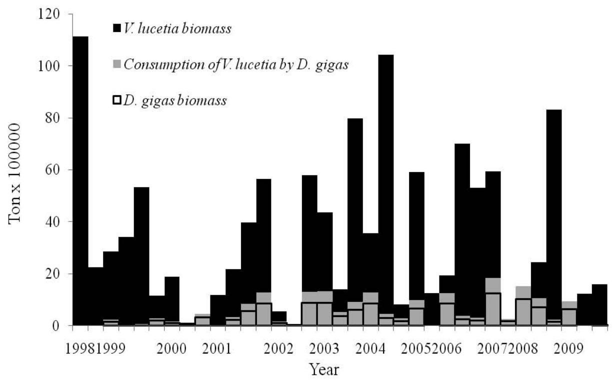

FIG. 4. – Acoustic biomass estimates of *D. gigas* and *V. lucetia* in the Humboldt Current System off Peru, and estimates of jumbo squid consumption on *V. lucetia*.

cording to the Q/B and the diet of *D. gigas*, predation on *V. lucetia* by *D. gigas* was of the order of 5% to 24% of the biomass estimate. The greatest predation impact by *D. gigas* was in 2008 with 23.3%, which means that the jumbo squid consumed 570 084 tons of *V. lucetia*. We averaged the diet consumption values (*DCij*=0.30), and using this value an estimate of jumbo squid consumption was made for 1998 to 2009 (Fig. 4). We should also highlight that there was a positive correlation between the biomass estimates of *D. gigas* and *V. Lucetia*. Accordingly, there was a moderate correlation throughout the entire series from 1999 to 2009 with an r^2 of 0.34 (90% confidence limits, P= 0.05). The biomass estimates of *D. gigas* and *V. lucetia* for 2007 and 2008 were used to contrast the trophic relationships. The regression value was less than the complete series (r^2= 0.28) but in both cases the regression values were positive. This shows that there is a moderate relation between *D. gigas* and the biomass of *V. lucetia*, which is expressed in the diet of the squid.

DISCUSSION

Jumbo squid sampled in 2007 and 2008 showed typical trophic behaviour: they fed on fish, cephalopods and crustaceans, and discarded the cannibalism. In general, studies on the feeding behaviour of jumbo squid are influenced by fishing activity because jumbo squid nibble fishery products, which has led to misconceptions about its feeding activity (Nigmatullin *et al.,* 2001, Markaida and Sosa-Nishizaki, 2003, Markaida, 2006, Ruiz-Cooley *et al.,* 2006, Field *et al.,* 2007, Rosas-Luis, 2007, Markaida *et al.,* 2008). However, when the data come from scientific sources, the results are more reliable: cannibalism is reduced or absent (Rosas-Luis, 2007), which is also reflected in this study. Samples of jumbo squid were taken on fishing cruises and the stomach contents were immediately frozen to preserve the tegument, scales and otoliths, which are the main structures used for identifying prey. The main group in the diet of the jumbo squid was found to be mesopelagic fish and the principal prey was the lightfish *V. lucetia*.

The acoustic biomass estimates made for *D. gigas* and *V. lucetia* are considered realistic because the target strengths were contrasted in situ with jig sampling of squid and fish trawls for *V. lucetia*. It is possible for acoustic signals to be misinterpreted; however different ways of obtaining the best signal for squid have been contrasted and it has been shown that the squid length is the best factor for obtaining the best target strength estimate (Castillo and Gonzales, 2000, Benoit-Bird *et al.,* 2008). In fact, other considerations can modify the final biomass values (sex proportion, maturity stage and size) but the error is not significant (Soule *et al.,* 2010). In mesopelagic fish is more difficult to identify the acoustic signal because different fish aggregate at the same time. However, in order to correctly estimate biomass the values obtained with the acoustic method can be contrasted with net trawls, in which the collected organisms are identified and analyzed. This provides a tool for verifying the fish composition in the water column (Marchal and Lebourges, 1996, Cornejo and Koppelmann, 2006). Both *D. gigas* and *V. lucetia* form aggregations. This characteristic and acoustic detection supported the hypothesis of a strong relationship between these two species, which is reflected in the jumbo squid's feeding activity (Fig. 2) and the vertical migrations shown in the echograms (Fig. 3).

Trophic relationships between *D. gigas* and *V. lucetia* are evident during the day and night and *D. gigas* probably feeds on *V. lucetia* in deeper waters. Alarcon *et al.* (2004) carried out experimental fishing with semipelagic trawls for lightfish and recorded large catches of jumbo squid. In research surveys of pelagic resources carried out by IMARPE, the jumbo squid catches also coincided with the detection of mesopelagic fish layers. The acoustic biomass estimates and echogram signals of *D. gigas* and *V. lucetia* in the water column suggest a close relationship between prey and predator, as the estimated distribution of jumbo squid near and offshore the continental shelf break overlapped with that of *V lucetia*. During the night, *D. gigas* was near the surface water surrounded by *V. lucetia* (Fig. 3). They were together until the first hours of the day when both *V. lucetia* and *D. gigas* moved to mid- and deeper water. They were in the same water layer during the day and returned to the surface water in the first hours of the night. This trophic relationship is reflected in the stomach content analysis of the squid, in which *V. lucetia* was the main component (Fig. 2). Evidently, jumbo squid prey on other species, such as the Peruvian anchovy (*E. ringens*) and other Myctophids, which were present in the stomach contents at the same time as *V. lucetia.* However, their abundance in the ecosystem is probably lower than that of *V. lucetia*. Moreover that *V lucetia* and *D. gigas* migrate to deeper waters during the day (migratory behaviour: Markaida *et al.,* 2005, Gilly *et al.,* 2006) and it is the factor that determines the dominance of *V. lucetia* in the squid's stomach contents.

Based on the stomach content analysis of *D. gigas* and the acoustic detection we can infer that *V. lucetia* was the main component of the jumbo squid's diet in 2007 and 2008 in the Humboldt Current System off Peru. As mesopelagic fish are important components of oceanic ecosystems, they are abundant and have a wide distribution in the ocean (Ahlstrom *et al.,* 1976). These characteristics of the group are evident in *V. lucetia,* one of the most important fish in the Humboldt Current System of Peru. It is found between 5° and 18ºS and can dominate the total catch in up to 68% of scientific cruises (Cornejo and Koppelmann, 2006). This dominance is expressed in other parts of the ocean. In the eastern tropical and subtropical Pacific this species has the third largest biomass after the northern anchovy *Engraulix mordax* and the Pacific hake *Merluccius productus* (Smith and Moser, 1988). The acoustic biomass estimates of *V. lucetia* and *D. gigas* made in the Humboldt Current System off Peru since 1998 show that there is a relation between the two species (Fig. 4). When there is a high biomass of *V. lucetia, D. gigas* has been observed to focus its feeding on this species (Table 3). Like other cephalopods, jumbo squid do not feeding selectively, which causes direct impacts on the biomass of the most abundant species present in the same water layer. Therefore, the importance of the prey species lies in its ability to support jumbo squid predation.

V. lucetia is a species with dynamic development that promotes rapid population growth, which is reflected in a high abundance and wide distribution in the ocean. If trophic relations in the ocean ecosystem are influenced by the distribution and abundance of prey groups and *V. lucetia* is an important mesopelagic component of this ecosystem, then it can maintain the biomass of different predators, even *D. gigas*. Due to these trophic relationships, an increase in *D. gigas* biomass may be the result of a similar increase in biomass in *V. lucetia*, which promotes a positive trophic effect as well as the development of other species in the ecosystem.

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