

The Humboldt Current squid *Dosidicus gigas* (Orbigny, 1835)

El calamar de la Corriente de Humboldt *Dosidicus gigas* (Orbigny, 1835)

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Abstract. We propose that the Humboldt Current squid and the Gulf of California squid are separate stocks and possibly subspecies of *D. gigas*. Data from 6,824 unsexed specimens from sperm whale stomachs and 43,256 sexed specimens from the fishery are used to try and increase our knowledge of the biology, life history and migrations of *D. gigas* from the Humboldt Current, and to make recommendations for the future management of the fishery, including a proposal that May and December be made closed seasons to protect the spawning squids.

Keywords: Gulf of California, Chile, Ecuador, Perú, life cycle, distribution, sperm whale, conservation.

Resumen. Proponemos que el calamar de la Corriente de Humboldt y el calamar del Golfo de California son poblaciones separadas y posiblemente subspecies de *Dosidicus gigas*. Datos de 6.824 especímenes, cuyos sexos no fueron determinados, de los estómagos de cachalotes y 43.256 especímenes de la pesca, donde los sexos fueron determinados, son usados para tratar de incrementar nuestro conocimiento de la biología, historia de la vida y migraciones de *D. gigas* de la Corriente de Humboldt, y hacer recomendaciones para el manejo futuro de la pesca, incluyendo la propuesta de que mayo y diciembre sean estaciones de veda para proteger a los calamares en desove.

Palabras claves: Golfo de California, Chile, Ecuador, Perú, ciclo de vida, distribución, cachalote, conservación.

'In view of the difficulties confronting international regulation, the only safe way forward is to seek agreement to an international moratorium on oceanic cephalopod fishing until more research can form a basis for rational exploitation'

MR Clarke (1996b)

Introduction

The present report is essentially a plea for rational exploitation of the Humboldt Current squid, which will safeguard, among other resources and the fishery, the recovery of the stock of sperm whales which feeds almost exclusively on *Dosidicus gigas* in the Southeast Pacific.

The Humboldt Current squid *Dosidicus gigas* (Orbigny, 1835) is the largest member of the family Ommastrephidae. In Chile it is called 'calamar pota' or 'calamar rojo', in Perú the fishermen call it 'pota' and the whalers call it 'jibia', and scientists call it 'calamar gigante'; in Japan it is called the 'Amerika-oorurume' and again, in Japan and in the U.S.A., it is the 'jumbo squid' or 'jumbo flying squid'. This animal is well figured by García-Tello (1964) and by Wormuth (1976).

We are here mainly concerned with the population which inhabits the Humboldt Current from the latitude of Tierra del Fuego, off the length of the coasts of Chile and Perú and so to the Galápagos Islands as the South Equatorial Current (Fig. 1): our concern with the population of *D. gigas*, which lives north of the

Humboldt Current in the Gulf of California and off the adjacent oceanic coastline, is essentially to show that it is probably separate from the southern population.

For centuries the artisanal fishery in Chile and Perú has included modest catches of *D. gigas*. Beginning with Russian expeditions in 1965 and 1968 (Nesis 1970) exploratory squid fishing was carried out from time to time until 1980 off Perú (Benites 1985¹, Benites & Valdivieso 1986) and off Ecuador (Icaza 1979), but none of these surveys, nor a report by Voss (1982)² on the possibilities for a squid fishery in Perú, resulted in a considerable industry. However in 1988 R Clarke *et al.* showed that sperm whales in the Humboldt Current were feeding virtually entirely on *D. gigas* and they were able to work out the daily ration of *D. gigas* consumed by the sexual classes of male and female sperm whales. They then applied these quantities to their assessment (1980) of the exploited stock of sperm whales in the Southeast

¹ Benites RC. 1985. Resultado de las investigaciones biológico-pesqueras de la jibia *Dosidicus gigas* (d'Orbigny, 1835) en el litoral peruano de julio 1983 a marzo 1984. Anales Congreso Nacional de Biología Pesquera, 28 de junio a 1 de julio, 1984, Trujillo, Perú. p. 10-16.

² Voss GL. 1982. Report on the possibilities for the development of a squid fishery in Perú. RSMAS University of Miami. 22 p. Mimeographed.

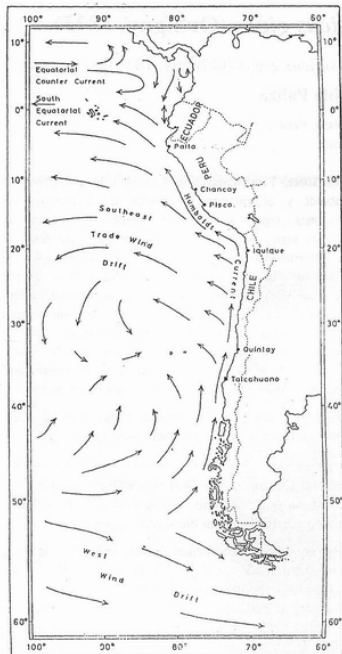


Figure 1

Whaling stations operating on the west coast of South America between 1959 and 1962. Surface currents of the Southeast Pacific, mainly after Schott, 1943, are also shown. (Reproduced from R. Clarke *et al.* 1968, Part I, Fig. 1)

Estaciones balleneras operando en la costa oeste de Sud América entre 1959 y 1962. También se enseñan las corrientes superficiales del Pacífico Sureste, mayormente según Schott, 1943. (Reproducida de R. Clarke *et al.* 1968, Part I, Fig. 1)

Pacific (Division 9 of the International Whaling Commission, 100°-60°W) between 1959 and 1960. They excluded from their original assessment for males those animals which in summer visit the Antarctic and feed on species of squid different from *D. gigas*; the assessment for females remained unchanged because female sperm whales do not visit the Antarctic: the revised figures emerged as 29,629 males (confidence limits 23,529 - 40,000) and 18,417 females (confidence limits 11,882 - 40,926). After applying the daily rations

by sexual classes the authors showed that the stock of sperm whales in the Humboldt Current between 1959 and 1960 was consuming each year 8.69 million tons of *D. gigas* (confidence limits 6.66 - 13.14 million tons) based on the normal complete meal, and 13.67 million tons (confidence limits 10.56 - 20.18 million tons) based on the complete meal to satiety (R. Clarke *et al.* 1988, p. 115-141, Tables 24-41). The immense size of the *D. gigas* population in the Humboldt Current was now revealed: accordingly, these authors proposed (p. 141) that a large scale fishery for *D. gigas*, using modern vessels equipped with automatic jigging machines, be established in the waters off Chile and Perú for domestic consumption and for export. Their report was distributed in the early months of 1989 and later in that year the Shinko Maru No. 2 arrived in Peruvian waters to undertake exploratory fishing for *D. gigas*, using both jigging machines and drift nets. She began the survey in early November about 90 miles from the Peruvian coast in 4° - 5°S, 82° 30'W and moved north with the current to the latitude of the Ecuadorian frontier, completing the fishing in the middle of December. The results were excellent (Instituto del Mar del Perú and Japan Marine Resources Research Center 1991, Rubio & Salazar 1992). A Russian fleet using drift nets also worked successfully off Perú, beginning in 1989 (Nignatullin *et al.* 1995). Further expeditions using jigging machines were sent from Japan and South Korea in subsequent years. The present great fishery for the Humboldt Current squid was now established.

When R. Clarke *et al.* recommended in 1988 a modern and intensive fishery for *D. gigas* they also recommended (p. 141) that research on the distribution and biology of this squid be intensified. Later, they recommended that a stock assessment be conducted on *D. gigas* throughout its range in the Southeast Pacific, by collaboration between the government institutes of Chile, Ecuador and Perú, and coordinated by the Permanent Commission of the South Pacific (R. Clarke *et al.* 1992³, 1993, R. Clarke & Paliza 1995, R. Clarke 1996). So far such a cooperative investigation has not been attempted.

Now, in reviewing for the present report the published work on *D. gigas*, it has become clear to us that the squid jigs are for the most part sampling only one segment, the earlier part of the life history of this large animal (Fig. 2). To sample animals larger than those taken on the squid jigs we must go to those found in the stomachs of sperm whales (Fig. 3). There are available thousands of measurements of these, and hundreds of weights, recorded during the whale

³ Clarke R., O. Paliza & A. Aguayo L. 1992. La pesca en desarrollo del calamar de la Corriente de Humboldt *Dosidicus gigas* y la recuperación de la existencia del cachalote *Physeter catodon* en el Pacífico Sureste. Resúmenes del X Congreso Nacional de Biología, 2-7 agosto, 1992, Lima, Perú, p. 173.

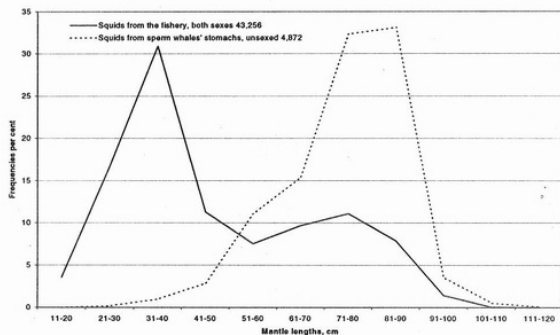


Figure 2

Relative frequencies of mantle lengths of *Dosidicus gigas*: unsexed from sperm whale stomachs in Chile and Perú (1959-62), and males and females combined from the fishery off Perú (1989-92). Squids from the fishery, both sexes 43,256. Squids from sperm whale stomachs, unsexed 4,872.

Frecuencias relativas de las longitudes del manto de *Dosidicus gigas*: sin sexos determinados de los estómagos de cachalotes en Chile y Perú (1959-62), y machos y hembras combinados de la pesca frente al Perú (1989-92). Calamares de la pesca, los dos sexos 43,256. Calamares de los estómagos de cachalotes, sin sexos determinados 4,872.

investigations conducted in Chile, Ecuador and Perú between 1958 and 1962. Unfortunately these squids were not sexed because at the time of the investigations they were of interest only as food of the sperm whale in the Southeast Pacific, and not as an exploitable resource. However, we believe that to some extent we have been able to overcome this disadvantage. We cannot wait for sexed specimens of *D. gigas* from sperm whale stomachs because the International Whaling Commission has prohibited sperm whaling from Chile and Perú since 1982.

After reviewing previous work the present report examines data from the fishery and data from sperm whale stomachs to try and increase our knowledge of the biology, life history and migrations of *Dosidicus gigas*, and to make a recommendation for the future management of this great fishery.

Material

Squids are most commonly measured as the 'mantle length', from the tip of the tail to the anterior end of the mantle. This is the measurement used in collecting data from the present fishery in the Humboldt Current. During the whale investigations in Chile and Perú, 1958-1962, the squids removed from the stomachs of sperm-whales were also often measured for 'standard length', being from the tip of the tail to the tip of the

longest arm. The 'total length', from tail to the tip of the longer tentacle, was only measured occasionally.

In the whaling stations at Paita (05°09'S, 81°08'W) and Pisco (13°46'S, 76°12'W) in Perú, and at Iquique (20°15'S, 70°08'W) and Talcahuano (36°40'S, 73°10'W) in Chile (Fig. 1), between 1959 and 1962 there were measured, from the stomachs of 2,403 sperm whale carcasses biologically examined, the mantle lengths of 4,872 specimens of *D. gigas*, the standard lengths of 1,952 and the total lengths of eight; at Pisco also the mantles of 821 of these squids were both weighed and measured, and the complete bodies of a further 228 were weighed and then measured for standard length. Altogether the data comprise 6,824 specimens of *D. gigas*. As earlier mentioned, no squids were sexed (Table 1).

The data available to us from sperm whale stomachs are from photographs of the whale investigation logbooks, made with the authorisation of the governments of Chile and Perú. The original logbooks are preserved by the government institutes in these countries.

We have also had occasion to refer to the 'Relaciones Semanales de Ballenas Cazadas' from the whaling stations of Chancay (11°36'S, 77°14'W) from 1959 to 1962 in Perú and of Iquique between 1961 and



Figure 3

Contents of the second stomach of whale Pa 12, male, 14.3 m, examined at Tierra Colorada, Paita, Perú on 21 June 1959. The first stomach had been destroyed by the harpoon. In the foreground are seen the remains of four squids *Dosidicus gigas*, between 1.2 and 1.5 m. in standard length. Behind are quantities of squid beaks, some with buccal muscles still attached, mixed with squid pens (*gladii*) and eye-lenses. A mass of pens, tangled with parasitic nematode worms, *Anisakis physeteris*, is below the lobe of the liver. The blubber hook leaning against the opened stomach wall is about 1 m long. (Photo: Robert Clarke).

Contenidos del segundo estómago de la ballena Pa 12, macho, 14,3 m, examinada en Tierra Colorada, Paita, Perú el 21 de junio de 1959. El primer estómago había sido destruido por el arpón. En el primer plano se ven los restos de cuatro calamares *Dosidicus gigas*, entre 1,2 y 1,5 m de longitud estándar. Atrás hay cantidades de picos de calamares, algunos con los músculos bucales todavía adheridos, mezclados con las plumas de calamares (*gladii*) y los lentes oculares. Una masa de plumas enredada con gusanos nemátodos parásitos *Anisakis physeteris* está abajo del lóbulo del hígado. Sobre la pared del estómago abierto está un gancho para tocino que mide aproximadamente 1 m. (Foto: Robert Clarke)

Table 1

Numbers of *Dosidicus gigas* measured, and weighed, from the stomachs of sperm whales examined at whaling stations in Chile and Perú between 1959 and 1962.

Cantidades de *Dosidicus gigas* medidos, y pesados, de los estómagos de cachalotes examinados en las estaciones balleneras en Chile y Perú entre 1959 y 1962.

Period	Paita		Whaling station		Totals
	Jun '59-Dec '61	Pisco Aug '60-Dec '62	Iquique Mar-Dec 1960	Talcahuano Mar-Jun 1961	
Mantle length	3263	1235	253	121	4872
Standard length	1088	740	114	10	1952
Total length		6	2		(8) ¹
Mantle length and weight		821			(821) ¹
Standard length and weight		228			(228) ¹
Totals	4351	3024	367	131	6824

¹ Numbers included in the totals measured for mantle length and standard length.

Table 2

Numbers of *Dosidicus gigas*, with mantle length measured and sexed, from the squid fishery off Perú between 1989 and 1992. The sex ratios are shown.

Cantidades de *Dosidicus gigas*, con longitudes de manto medidas y con sexos determinados, de la pesca de calamares frente al Perú entre 1989 y 1992. Se muestra la relación de sexos.

Vessel(s) and months fishing	1989		1990		1991		1992		1989-1992		Sex ratios by vessel(s) ♂ : ♀
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Shinko Maru 2 Nov-Dec	349	3185							349	3185	1:9.13
Nansen Mar-Apr			633	861					633	861	1:1.36
Kwang Yang 108 Jul-Aug			521	3154					521	3154	1:6.05
Japanese vessels Oct-Nov					1006	3330			1006	3330	1:3.31
Apr-Sep							2376	9772	2376	9772	1:4.11
Korean vessels Oct-Nov-Dec					1254	3413			1254	3413	1:2.72
Jan-Sep							3336	10066	3336	10066	1:3.02
Totals	349	3185	1154	4015	2260	6743	5712	19838	9475	33781	Total squids 43,256
Sex ratios	1:9.13		1:3.48		1:2.98		1:3.47		1:3.57		

1962 and of Talcahuano during 1962 in Chile, there being no other 'Relaciones' available to us. The 'Relaciones' give the positions where sperm whales were caught and (except at Talcahuano) the surface water temperatures at these positions.

Data from the squid fishery comprise the mantle lengths of 43,256 sexed specimens of *D. gigas* from Japanese and Korean vessels fishing off the coast of Perú between 1989 and 1992 (Table 2).

Size range

Mantle lengths of *D. gigas* from the exploratory fishing off Perú in 1968 were measured to an accuracy of ± 1 cm by Nesis (1970) and presumably later observers have done the same. The mantle lengths of animals from sperm whale stomachs examined by different biologists at different whaling stations in Chile and Perú between 1959 and 1962, were measured to accuracies between ± 1 cm and ± 10 cm. Therefore, to compare the size ranges of these two groups, we have put the mantle length interval at 10 cm for both the 43,256 squids from the fishery off Perú, with males and females combined, and the 4,872 unsexed squids from sperm whale stomachs (Fig. 2). The largest mantle lengths of the latter group are some 10 cm longer than the largest mantle lengths from the fishery, but the modes are very different, being at 35 cm for the fishery with a secondary mode at 75 cm, whereas the animals from sperm whale stomachs show a single mode at 75-85 cm, corresponding to the secondary mode for animals from the fishery, but very pronounced.

Among cephalopods, males are generally smaller than females (Pelseneer 1906), and *D. gigas* is no exception. Nesis (1970, p. 112) observed that in this squid the maximum mantle length of females taken by fishing exceeded that of males by 10%, and the average mantle length was 6% greater in females. Rubio & Salazar (1992) and Fusejima (1993) showed that the modes in the frequency curves of mantle lengths in females were respectively 2 cm and 2-3 cm in advance of those of males.

Fig. 4 shows the mantle length frequencies of males and females in the present material from the fishery. The principal mode for females at 33 cm is 2 cm in advance of that for males at 31 cm. And the maximum mantle length of females is seen to be some 6 cm greater than that for males.

There have been various observations and proposals on the maximum size and weight of *D. gigas*. Duncan (1941), sport fishing off Cabo Blanco, Perú, took specimens of *D. gigas*, one of which was nearly 9 ft (2.7 m) in length and weighed over 100 lb (45 kg). Lane (1957, p. 131) records that scientists from the University of Miami told the late Dr Gilbert L. Voss that these squids grow to an over-all length of some 12 ft (3.7 m) and a mantle length about 6 ft (1.8 m) and weigh up to 350 lb (160 kg). Voss & Sisson (1967) again mentioned squids up to 120 kg (264 lb) taken from Viña del Mar in Chile. García-Tello (1965) found that specimens fished off Valparaíso had mantle lengths to 0.93 m (3 ft) and

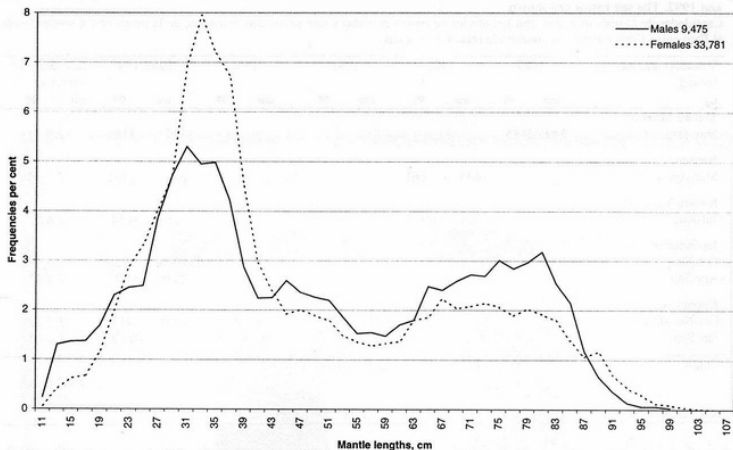


Figure 4

Relative frequencies of mantle lengths compared in male and female *Dosidicus gigas* fished off Perú (1989-92).

Frecuencias relativas de las longitudes del manto en machos y hembras de *Dosidicus gigas* pescados frente al Perú (1989-92).

weights to 35.2 kg (77 lb). MR Clarke (1966, p. 117) was told by correspondents in Chile that *D. gigas* may grow to a total length of 12 ft (3.7 m). Nesis (1970) said that some of the *D. gigas* beaks taken in Sigsbee trawls were of such a size that they must have belonged to animals exceeding 50 kg in weight. MR Clarke *et al.* (1976) identified a collection of squid beaks from sperm whale stomachs examined in Chile and Perú; the largest beak, belonging to *D. gigas*, came from an animal estimated to weigh more than 50 kg. R Clarke *et al.* (1978, p. 163) fished for *D. gigas* during night stations off the coast of Chile: the largest individual seen under the lamps was about 2.5 m (8 ft 6 in) in standard length. Roper *et al.* (1984) said that off Chile *D. gigas* has a maximum total length of 4 m (13 ft) and a maximum mantle length of 1.5 m (5 ft). And, as Lee (1875, p. 107) has recorded, Molina's '*Sepia tunicata*' (1782, 1788) weighed 150 lb (68 kg) and this could have been a specimen of *D. gigas*, or possibly *Taningia danae*.

Most of these measurements and estimates seem reasonable enough except for the weights of 160 kg and 120 kg which we consider to be exaggerations, and

some of the lengths are hearsay evidence or of squids seen in the water. Among the 6,824 specimens of *D. gigas* examined during the whale investigations in Chile and Perú between 1959 and 1962 the longest mantle measured was 1.20 m (4 ft) at Paita in February 1960 and the greatest standard length was 2.06 m (6 ft 9 in) at Iquique in Oct 1960, whilst at Pisco the heaviest entire *D. gigas* weighed 58 kg (128 lb) in May 1962. The data presented here on squids from sperm whale stomachs do not go beyond 1962, but at Pisco the whale investigations were prolonged through 1963. In that year Vinatea (1965)⁴ examined a *D. gigas* measuring 2.20 m (7 ft 3 in) in standard length and weighing 65 kg (143 lb). Now we know that a male sperm whale of 14.2 m (47 ft), which is of no great size, can swallow whole a much larger squid (*Architeuthis* sp.) weighing 184 kg, with mantle length 1.98 m, standard length 4.96 m and total length 10.49 m (R Clarke, 1955). So we may with some confidence say that the squid with the longest

⁴ Vinatea E. 1965. Estudio cuantitativo del contenido estomacal del cachalote (*Physeter catodon*) en el área de Pisco (1961-1962). Tesis de Bachiller. Universidad Nacional Mayor de San Marcos, Lima. 101 p. (unpublished).

mantle of 1.20 m (4 ft) among the 6,824 squids from sperm whale stomachs between 1959 and 1962, and the squid with the longest standard length of 2.20 m (7 ft) measured in 1963 and weighing 65 kg (143 lb), represent the largest sizes and weight attained by *D. gigas*. We hesitate to suggest a maximum total length because of the elasticity of squid tentacles. However, among the eight *D. gigas* measured for total length during the whale investigations the squid with the greatest total length of 2.60 m had a mantle length of 1.18 m; then the total length of a specimen of maximum mantle length 1.2m should be $2.60 \times 1.2/1.18 = 2.64$ m (8 ft 9 in) and this we propose for the maximum total length.

Weight/length equations

When investigating the biomass of squids it is necessary to estimate the weights of squids which have been measured but not weighed, as, for instance, in R Clarke *et al.*'s estimate (1988, p. 87-90, Fig. 11) of the weight of *D. gigas* consumed each year by the estimated population of sperm whales in the Southeast Pacific between 1959 and 1962.

In the fishery, squids are normally measured as the mantle length. Table 3 gives the results from various workers of the regressions of total or partial body weight on mantle length for *D. gigas* expressed as $W = aL^b$, where W is the total or partial body weight, a is a constant, L is the mantle length and b is the regression coefficient. Calculations were made in the logarithmic transformation, $\log W = \log a + b \log L$. Table 3 also includes the results from squids removed from sperm whale stomachs in the Southeast Pacific between 1959 and 1962, where the 6,824 flesh remains consisted of headless bodies of squids measured as mantle lengths, head-and-arms measured as such, and entire squids measured as standard lengths, the tentacle lengths being ignored: here the regressions of the specimens weighed at Pisco were made on these three different lengths. The units for squids from the fishery are in grams and millimetres, whereas those for squids from sperm whale stomachs are in kilograms and metres. Thus in squids from the fishery the body weights were increasing at $b \times \log$ mantle weight (grams) per log millimetre increase in mantle length. In squids from sperm whale stomachs the weights of the entire squid or its parts were increasing at $b \times \log$ weight (kilograms) per log metre increase in mantle length, head-and-arms length or standard length. However the regression coefficients b are comparable.

We prefer not to comment on the regression coefficients obtained by Erhardt *et al.* (1983) from the Gulf of California compared with those by authors from the fishery off Perú because it will be seen that we believe that the populations of *D. gigas* north and south

of the equator are separate and distinct, possibly subspecies.

Benites (1985, footnote 1) obtained a larger regression coefficient, 3.42, in March 1984 than in September 1983 where the coefficient was 2.82. He attributed this to numbers of small squids in March, but it may well have been due to the presence of females heavy with eggs. Benites & Valdivieso (1986) obtained a coefficient of 3.06 from males and females combined off Perú, but the coefficient for spawning females was only 2.18: presumably these were spent females, for had they been about to spawn we would have expected a higher coefficient because of their heavier weight. As much may be said for the results of Rubio & Salazar (1992) on total weights for males and females separately: these authors obtained regression coefficients of 2.91 for males and 2.71 for females, whereas we should expect males to have the lesser coefficient, because in November-December many females are about to spawn or spawning. However, the coefficient for mantle weight in females, 2.87, is indeed greater than that in males, 2.72.

The coefficient of 1.83, for total weight for males and females combined from sperm whale stomachs, is noticeably smaller than the coefficient of 3.06 obtained by Benites & Valdivieso for males and females combined from the fishery. This is explicable if the large squids from sperm whale stomachs were growing at a faster rate, and, indeed, Fusejima (1993) has found that after 30 cm mantle length the growth rate does increase (Table 3). However it will be seen that we have needed to assume for males and females a constant growth derived from Masuda *et al.*'s results (1998) from statoliths of *D. gigas*.

Another weight/length equation using this time the beaks of *D. gigas* has been elaborated by García-Tello (1965), based on the method developed by MR Clarke (1962). Applying the equation $W = aRL^b$ García-Tello obtained the following regression of total body weight on the rostral length of the lower beak, RL, from 146 specimens of *D. gigas* fished off Valparaíso,

$$W = -2.054 RL^{2.487}$$

Where W is the total weight of the squid in kilograms, -2.054 is the constant a , RL the rostral length of the lower beak in millimetres and 2.487 is the regression coefficient b . MR Clarke *et al.* (1976) will have employed this equation, or something similar, when they showed that, in a random sample of beaks from sperm whale stomachs from Chile and Perú, the largest beak from *D. gigas* must have come from a specimen weighing over 50 kg.

Table 3

Regressions of total or partial body weight on mantle length for *Dosidicus gigas* expressed as $W=aL^b$ where W is the total or partial weight, a is a constant, L the mantle length and b the regression coefficient.

Regresiones del peso del cuerpo total o parcial, sobre la longitud del manto para *Dosidicus gigas* expresado como $W=aL^b$ donde W es el peso total o parcial, a es una constante, L es la longitud del manto y b es el coeficiente de regresión.

References	Locality and months	Sample size	Mantle length range	Equation	Remarks
Erhardt <i>et al.</i> (1983, p. 325)	Gulf of California, Mexico. Apparently all months in 1980		18 – 72 cm	$W=0.02646165L^{2.989379}$ $W=0.01775312L^{2.940475}$ $W=0.02503828L^{2.937908}$	Total weight Mantle weight Mantle and head weight
Benites (1985, p. 11)	Off coast of Perú. Sep 1983, Mar 1984	91. Presumably both males and females	17 – 32 cm	$W=0.0000741L^{2.820}$	Total weight, Sep 1983
		259. Presumably both males and females	14 – 35 cm	$W=0.000002399L^{3.423}$	Total weight, Mar 1984
Benites & Valdivieso (1986, p. 118 and Fig. 8)	Off coast of Perú. Sep, Oct and Dec 1979. Apr 1980	341. Both males and females	7 – 39 cm	$W=0.00001903L^{3.0648}$ $W=0.0036377L^{2.18}$	Total weight Total weight in spawning females
Rubio & Salazar (1992, p. 7. Table 13)	Off coast of Perú. Nov-Dec 1989	175 males		$W=0.000045L^{2.909317}$ $W=0.000079L^{2.723706}$	Total weight Mantle weight
		234 females		$W=0.000156L^{2.710699}$ $W=0.000033L^{2.872775}$	Total weight Mantle weight
Fusejima (1993, p. 9, Fig. 20)	Off coast of Ecuador and Galápagos Islands. Nov-Dec 1992	Both males and females 268 in November 322 in December		No equation given	Two graphs in his Fig. 20 for Nov and Dec. Observed that after 30 cm mantle length the growth rate increased
R Clarke <i>et al.</i> 1988, p. 87, Fig. 11	Pisco, Perú. From the stomachs of sperm whales 1961, 1962. All months	Both males and females			
		801	Mantle length	$W=24.55L^{2.01}$	Mantle weight only
		347	Length of head-and-arms	$W=11.48L^{1.65}$	Head-and-arms weight
		172	Standard length The standard length range was 0.42-1.90 m.	$W=12.59L^{1.83}$	Total weight

Using essentially the same equation Nesis (1970) has employed the beaks of *D. gigas* to estimate the corresponding mantle lengths. From 50 specimens he obtained the regression of mantle length on the rostral length of the upper beak,

$$ML = 6.3 RL^{0.8}$$

where ML is the mantle length in centimetres, 6.3 is the constant a , RL is the rostral length in millimetres and 0.8 the regression coefficient b .

Horizontal distribution

Tafur & Rabi (1997) say that *D. gigas* 'is widely distributed across the eastern Pacific'. This distribution is sweeping enough, but MR Clarke (1966) gives references to identifications as far afield as Australia, the Solomon Islands and the Red Sea, and these we think should be checked. However, several authors are agreed that the species extends off the west coasts of the Americas from California at about 35°N to the latitude of Tierra del Fuego at 55°S (Roper *et al.* 1984, Benites & Valdivieso 1986, Fernández & Vásquez 1995): Nesis (1970) gave from California only as far as Isla Chiloé in Chile, but included specifically the Galápagos and Juan Fernández Islands. Erhardt *et al.* (1983, p. 308) and Wormuth (1998, p. 378) gave approximately 36°N to 26°S and westward up to 125°W. Yamashiro *et al.* (1998) extended this westward distribution to 140°W in its broadest part.

All these observations suggest that the distribution of this squid is continuous, but we take a somewhat different view, already outlined by R Clarke (1966). We believe that the populations of *D. gigas* north and south of the equator are separate and distinct, possibly even subspecies. In the south this squid lives in the cold Humboldt Current from its beginning off Tierra del Fuego (Fig. 1) northwards off the coasts of Chile and Perú until about 4°S off Cabo Blanco where the Current turns westward to bathe the shores of the Galápagos Islands as the South Equatorial Current. Specimens of *D. gigas* (called *Ommastrephes gigas*) were taken off the Galápagos Islands at 00°17'S 74°12'W early in November 1959 (R Clarke 1962) and MR Clarke (1966) gives an earlier report from the Galápagos by Boone (1933) which we have not seen. Further, from the results of R Clarke *et al.* (1988) on the feeding of sperm whales in the Southeast Pacific, we are in no doubt that *D. gigas* was the squid 'four or five feet in length' which Colnett (1798, p. 147) found to be the principal food of sperm whales around the Galápagos Islands. The warm Equatorial Counter Current, which bathes the coasts of the extreme north of Perú, Ecuador and Colombia, forms a barrier to the penetration further north of this southern population of *D. gigas*. During the winter and spring months of the northern hemisphere the northern population is mostly concentrated in the warm waters of the Gulf of California. In the summer and autumn part of this population spreads out of the Gulf northwards as far as California and southwards off the Mexican coast (Erhardt *et al.* 1983, Figs. 4 and 5). Clark & Phillips (1936) described this squid's occurrence off California. We should expect that specimens of *D. gigas* which may occur off Central America, Colombia and coastal Ecuador belong to this northern population.

We judge this to be the distribution of the two

populations in normal years. When the annual 'El Niño' phenomenon takes place, normal or acute, the Equatorial Counter Current spreads southwards so we should not expect the southern population to reach so far north.

We now try to substantiate our proposal for two separate populations of *D. gigas* north and south of the equator. Wormuth (1976, p. 38) makes the following observations on *D. gigas*.

'*D. gigas* provides the first indication of geographical variability. More than 800 specimens from north of the equator are in the SIO [Scripps Institution of Oceanography] collections. Of these only five exceed 300 mm mantle length; the largest is 396 mm ML. The SIO collections contain seven specimens (from a total of 80) over 300 mm ML from south of the equator, the largest being 610 mm MLOff Perú animals of 1.5m ML are not uncommon.....This difference in size may only be the result of a pronounced difference in food supply, but there are indications that other morphological differences exist. Although better collections are needed from the southern area for detailed comparative work, preliminary data show a difference in the number of sucker rows on arm 1 between specimens from north and south of the equator. Other differences may be found in a more detailed study.....'

Wormuth goes on to give in his Table 8 a comprehensive study of the morphometry of the northern population: it is hoped that government institutions in Chile, Ecuador and Perú will prepare similar tables for the southern population of *D. gigas* for comparison with Wormuth's Table 8.

Recently Wormuth (1998, p. 378) has returned to these differences between *D. gigas* north and south. He says:

'Significant morphometric changes occur in this species from north to south. Specimens from the southern area have proportionately longer arms relative to mantle length (Fig 2) as well as more suckers per arm. In other pelagic species of this subfamily no such increase in the number of suckers per arm with increasing mantle length occurs once an individual reaches sexual maturity (Wormuth, unpublished data).'

Roper *et al.* (1984) also remarked on the smaller body size in the northern population. And it is significant that Erhardt *et al.* attributed the rapid growth observed in the northern population to 'the fact that the waters of the Gulf of California present *high temperatures* [our italics] and high food availability, almost all the year round.' Sato (1976), after observing that off the west coast of Baja California the fishing grounds were over the continental slope and especially at the convergence of coastal and offshore currents,

went on to say that 'with the lowering of the water temperature the squid seemed to migrate to warmer areas.' Finally Erhard *et al.* concluded that the 'population of giant squid in the Gulf of California is clearly a single stock with multiple cohorts.'

Exploratory fishing for *D. gigas* off the continental coast of Ecuador and round the Galápagos Islands has been conducted on three occasions. Nesis (1970, Fig. 1) reported good catches west and northwest of Guayaquil in 1968. We would consider these squids to belong to the northern population. Icaza (1979) reported indifferent catches, but Fusejima (1993) obtained extremely poor results off the continental coast and round the Galápagos. This expedition was round the Galápagos in December, so that normal 'El Niño' conditions in this month could have accounted for the absence of *D. gigas* off the islands. In spite of Nesis' good catches off Guayaquil in 1968, we would not expect much abundance of *D. gigas* off the continental coast of Ecuador in normal years.

Coming now to the southern population of *D. gigas* we briefly review the positions of captures and corresponding sea temperatures from the fishery.

Nesis (1970) said 'We observed the largest number of squid from the equator to 18°S and from the edge of the continental shelf to 200-250 miles from the shore.....; their numbers were also few over the shelf, and they decreased sharply in abundance beyond 250-300 miles from the continent'. In a later paper Nesis (1983) said that *D. gigas* was most abundant at surface temperatures of 17-23°C in the southern hemisphere compared with 25 - 28°C in the northern hemisphere. Off Perú in March 1984, in what Benites (1985, footnote 1) considered to be normal conditions, fishing was conducted between 5° and 7°S with surface temperatures between 19°C near the coast and 25°C about 100 miles to seaward. Benites & Valdivieso (1986) found most squids between 30 miles off Talara and 350 miles off Chimbote; they gave a temperature range of 17.5° - 27.5°C. Rubio & Salazar (1992) found the greatest concentrations between 3°30'S and 5°S and 85-110 miles from the coast; they noted that the squid tended to be localised where oceanic water at 20°-21°C penetrated into coastal water at 17.8-19.6°C. Yamashiro *et al.* (1995)⁵ gave the best fishing off Perú for *D. gigas* during January to November 1995 as between 3° and 5°S up to 100 miles from the coast and with surface temperatures greater than 18°C. Mariátegui & Taipe (1996) found that this squid between 1991 and 1994 was distributed between 03°30' and 16°35'S at 20-180 miles from the coast, the greatest concentrations being between 4° and 6°30'S at 40-60 miles from the

coast. In 1995 Segura *et al.* (1996) explored between 3°34'S (opposite Puerto Pizarro) and 7°53'S (Chicama) and obtained the best catches between 50 and 120 miles from the coast where surface temperatures were greater than 18°C. Yamashiro *et al.* (1997) further surveyed the distribution of *D. gigas* in the north of Perú between 1991 and 1995; this squid was found between 30 and 210 miles from the coast, with the greatest concentrations at the confluence of warm and cold water masses, the surface temperatures being greater than 18°C. Again Kuroiwa (1998) found that fishing grounds for *D. gigas* with a high catch per unit of effort are 'usually located where a thermocline lies at 10-50 m deep with water temperature 14°-15°C at 50 m-stratum.'

Less information is available to us from Chile. From observations off Iquique around 20°S in April-May 1956, de Sylva (1962) observed that *D. gigas* occurred 'in the inshore green water and in the offshore blue water, but it seemed more abundant close to shore', which we interpret as being more abundant in cool water. Fernández & Vásquez (1995) discussed the fishery for *D. gigas* off Chile between 1991 and 1994 and noted that fishing was mostly concentrated between 29° and 34°S, but they did not mention distances from the coast nor surface temperatures.

Similar information on positions and surface temperatures is available for the large and very large specimens of *D. gigas* from the stomachs of sperm whales landed in Chile and Perú. Sperm whales are in the Southeast Pacific to feed on *D. gigas* which is virtually their only food in these waters (R Clarke *et al.* 1988, p. 93). So where the sperm whales were taken, there were the *D. gigas*. Fig. 5 shows the percentage frequencies of the surface temperatures recorded at positions where 118 sperm whales were captured from Chancay (11°36'S, 77°14'W) during 1959-62 off Perú, and where 429 sperm whales were captured from Iquique (20°15'S, 70°08'W) during 1961-62 off Chile. Fig. 5 is constructed from data in the 'Relaciones Semanales de Ballenas Cazadas': the 'Relaciones' from Talcahuano do not include surface temperatures and the 'Relaciones' from other whaling stations in the Southeast Pacific are not available to us. The temperatures in Fig. 5 range from 15° to 26°C with a peak at 19°-20°C opposite Chancay, and from 11°C to 27°C with peaks at 17°-18°C and 21°-22°C opposite Iquique. The positions of capture of the sperm whales ranged from 10° to 12°S and from 77°47' to 80°20'W off Chancay, and from 18° to 23°S and 70°20' to 75°16'W off Iquique (Fig. 1).

⁵ Yamashiro C, L. Mariátegui, J. Rubio, J. Argüelles & R. Tafur. 1995. Situación actual del Calamar Gigante y perspectivas de explotación para 1996. Instituto del Mar del Perú, Callao, 7 p. (unpublished)

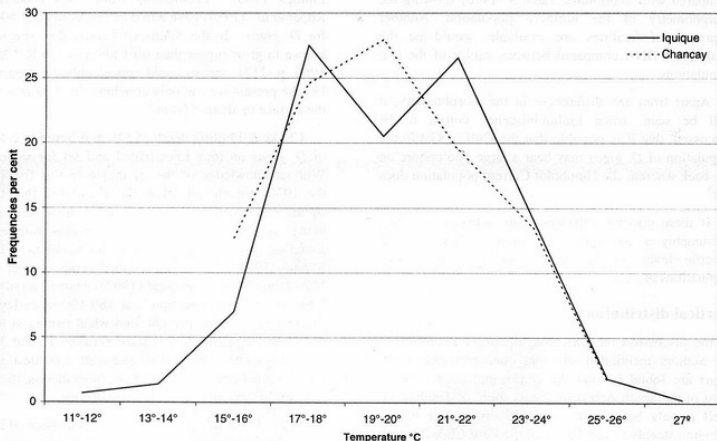


Figure 5

Relative frequencies of the sea surface temperatures at positions where 118 sperm whales were captured from Chancay during 1959-62 in Perú, and where 429 sperm whales were captured from Iquique in Chile during 1961-62.

Frecuencias relativas de las temperaturas de la superficie del mar en las posiciones donde se capturaron 118 cachalotes desde Chancay en el Perú durante 1959-62, y donde se capturaron 429 cachalotes desde Iquique en Chile durante 1961-62.

Now the above review on *D. gigas* from the fishery, and Fig. 5 associated with *D. gigas* from sperm whale stomachs, may be compared with Gunther's detailed account (1936) of the Perú Coastal Current, which we call the Humboldt Current. The surface temperatures associated with *D. gigas* from the fishery, and with the positions of capture of sperm whales feeding on *D. gigas*, range from 11°C to 27°C and all are within the range of surface temperatures in the Current given by Gunther, principally in his Figs 29 and 30 for lines of stations perpendicular to the coast between Cape Carranza in Chile and Santa Elena in Ecuador. Similarly, the positions of capture of *D. gigas* in the fishery, ranging from 20 to 350 miles from the coast, and the positions of capture of sperm whales from Chancay and Iquique, all come within Gunther's Table XXI showing the 'Supposed western boundary of the Perú Coastal Current' between the equator and 40°S. The higher temperatures we have reviewed, say between 20°C and 27°C, will refer to the confluence of oceanic and coastal waters, mentioned by several authors in Gunther's review, not only on the western edge of the

Current, but in the Current itself where tongues and swirls of oceanic water intervene in the upwelling zones; Gunther was at pains to insist on these local irregularities in the Current in his p. 195-218. Such confluences seem to attract high concentrations of *D. gigas*.

Further, we shall later show that the spawning peaks of the northern and the southern populations of *D. gigas* are the same in season but opposite in time.

Summarising, the southern population of *D. gigas* is restricted to the cool water of the Humboldt Current from far south in Chile to its extension as the South Equatorial Current to the Galápagos Islands and beyond. Its distribution further north is restricted by the warm Equatorial Counter Current. The northern population lives in warm water and the squids are smaller than those of the southern population. We here distinguish the two populations as the Humboldt Current squid and the Gulf of California squid, while both retain the same specific name *Dosidicus gigas* until such time as morphometric data from the southern population may be

compared with Wormuth's Table 8 (1976) showing the morphometry of the northern population. Another approach, if facilities are available, would be the analysis of DNA compared between squids of the two populations.

Apart from any differences in the morphometry, it will be seen, when bioluminescence comes to be discussed, that it is possible that the Gulf of California population of *D. gigas* may bear a large photophore on the back whereas the Humboldt Current population does not⁶.

If these possible differences are substantiated then presumably a taxonomic separation, at least to sub-specific level, would be appropriate in these two populations of *D. gigas*.

Vertical distribution

In the discussion on horizontal distribution several of the authors mentioned say that concentrations of *D. gigas* are found beyond the continental shelf. Along most of the South American coast south of Tumbes the shelf is only between five and 15 miles wide before plunging steeply to the depths of the Perú-Chile Trench. So in the Humboldt Current *D. gigas* typically lives over deep water.

R Clarke *et al.* (1988, p. 101-2) have already reviewed most of what is known of the vertical distribution of *D. gigas* and it is appropriate to reproduce their discussion here :

'Since the sperm whale in the Humboldt Current feeds virtually entirely on *Dosidicus gigas* we need to try and find out the vertical range of this species. It is well known to frequent the surface at night where it has been observed by many authors including Duncan, 1941; R. Clarke, 1962; García-Tello, 1964; Nesis, 1970 and R. Clarke *et al.* 1978. It may occur near the surface during the day (Roper & Young, 1975) and even at the surface, for the squid observed by Beale (1839, p. 66) to rise briefly to the surface one day off Paita Head was almost certainly a *D. gigas*. Wilhelm (1960⁷, unpublished) saw great schools of *D. gigas* at the surface between 40 and 100 miles from the coast but did not specify whether at night or in the day. A North Pacific stock of *D. gigas* has been located hydroacoustically at depths greater than 100 m. when migrating into the Gulf of California (Erhardt *et al.* 1983). The species has been caught on baited hooks as deep as 300 fathoms or 549 m. (Clark &

Phillips 1936). Presumably from this observation Roper *et al.* (1984) gave a maximum depth of ' ? 500 m' for *D. gigas*. In the Southeast Pacific the species is known to grow bigger than off California (M.R. Clarke, 1966, p. 117), and so could conceivably go deeper..... For the present we can only conclude that it ranges from the surface to about 550 m.'

Clarke & Phillip's depth of 549 m referred to catches of *D. gigas* on long lines baited and set for sablefish. Without knowledge of the technique in this fishery in the 1930s we should allow the possibility that these squids were caught at lesser depths when the lines were being hauled. Certainly recent observations using echosounding give no results approaching 550 m. Thus, Benites (1985, footnote 1) obtained depths greater than 150 m; and Rubio & Salazar (1992) obtained a range of 3 to 270 m, with most squids at 180-190 m during the day and at 30-50 m at night, and when fishing at night under the lamps, the squids were between 10 and 30 m deep. So we here revise R Clarke *et al.*'s greatest depth for *D. gigas* from 550 m to 300 m. Nonetheless, there is a possibility that the species can go deeper.

R Clarke *et al.* (1988, p. 103) have been able to show that *D. gigas* has a pattern of ontogenetic descent, that is to say the squids penetrate to deeper levels as they grow older and bigger. These authors found that lactating sperm whales were feeding on smaller squids than those eaten by recently ovulated whales, resting whales and pregnant whales: they suggested 'that lactating whales, hampered by the limited diving range of their calves, feed nearer to the surface than other mature females, and at this level the lactating whales encounter smaller, younger squid'. They pointed out, of course, that stratification by size could not be permanent because at night in the Humboldt Current large sizes of *D. gigas* rise to the surface. They said that 'during the daytime the species is probably distributed down the water column according to age and size, and the large *D. gigas*, which go deepest, may find at these levels other species of squid to feed upon.' When we come to discuss the food of *D. gigas* we shall identify these other species of squid.

Colour

D. gigas when fished has a reddish colour, but once on deck it shows spectacular changes in colour, as indeed do many other cephalopods. R Clarke *et al.* (1978, p. 165) when fishing off Chile noted that 'One specimen [of *D. gigas*] at Station I₂₄ showed the following changes over the mantle within three minutes of reaching the deck: lead-brown, deep crimson, ochre, dirty cream, brick-red and reddish-brown'.

These changes are due to the expansion and

⁶ An anonymous referee tells us that he has found no large photophore on the backs of about 1,000 Gulf of California squids examined.

⁷ Wilhelm O 1960. *Dosidicus tunicata* (Molina, 1788) frente a las costas de Chile. Paper presented to the Primer Congreso Chileno de Zoología, Santiago de Chile, 14-17 setiembre 1960. 5 p. (Unpublished)

contraction of differently coloured chromatophores in the skin, probably accompanied by the reflective action of iridocytes. But *D. gigas* is also known to show bioluminescence.

Bioluminescence

García-Tello (1964) observed that off Chile when *D. gigas* was landed on the deck in darkness the squids glowed in a series of points on the arms and head, and these points shone with an intense blue light and with the brilliance of diamond. The shining did not last for more than one or two minutes. García-Tello noted that Roper (1963) had mentioned subcutaneous photophores in *D. gigas*, but apparently this was the first record of their functioning. MR Clarke (1965) looked for photophores in preserved material of *D. gigas* but without success, but he was looking for a large, complex light organ on the back of the squid which he described in detail from other Ommastrephids. Steenstrup (1881) had earlier said that this organ also occurred in *D. gigas* although Steenstrup did not at the time recognise its photogenic nature. Nesis (1970) found 'subcutaneous luminescent organs' as elongate or oval granules, mostly 0.4-1.4 mm long, in much the same places on the head and arms where García-Tello saw the shining of bioluminescence. But Nesis never saw any of these squids shining. He said 'Evidently this species glows only "when it feels like it", and not when hunting prey, but most probably during reproduction'. However, it is likely that Nesis saw no bioluminescence because industrial squid fishing is always carried out using powerful overhead lighting, and García-Tello says he only saw the shining of the squids when the lights on deck were all extinguished.

MR Clarke (1965) proposed that in the surface waters of all oceans each of the species of Ommastrephidae, including *D. gigas*, comprise 'two partially sympatric species, one with and one without a large photophore on the back'. We have not seen Steenstrup's paper of 1881, but if his specimens of *D. gigas*, bearing the photophore, came from the Gulf of California population whilst those without the photophore, examined by MR Clarke, came from the Humboldt Current, there would be a further difference between these two populations of *D. gigas*. In any case there seems to us to be some confusion regarding bioluminescence in *D. gigas* and the matter could with profit be further investigated.

Food

Table 4 records the stomach contents observed by previous workers in *D. gigas* from the fishery. The variety of organisms encountered demonstrates the precision of Nesis's summing-up (1970): '*Dosidicus* is

a typical schooling nektonic predator, which eats any prey that moves, provided only that it is abundant and of convenient size.'

There seems to be no difference between the kinds of food eaten by the Gulf of California squid and the Humboldt Current squid except that red crab (the pelagic Anomuran *Pleuroncodes sagaz*) is not recorded from the Humboldt Current squid. Possibly red crab does not extend to the southern hemisphere. Erhardt *et al.* (1983, p. 319) say that 'In the areas where upwellings are not strong enough to support large populations of pelagic fishes the principal diet consists of bathypelagic fishes, particularly Myctophids'. If this were so, one might expect less mention of Myctophids in stomachs from the Humboldt Current squid, but whereas Wormuth (1976) does specifically identify these lantern fishes from Gulf of California squid, they are mentioned twice from Humboldt Current squid, by Nesis, giving their presence in 70.2% of stomachs, and by Benites & Valdivieso (1986).

Lantern fishes are interesting because they live deep in the day and come to the surface at night, which must at least partially explain the presence of *D. gigas* near the surface at night.

Further regarding food, Lane (1957, pp. 36, 148) says that *D. gigas* squids cause a considerable damage to the coastal fishery for yellowfin tuna (*Thunnus albacares*) off Chile and Perú: they attack hooked tuna of 50-60 lb and eat all but the heads. It will be seen later that yellowfin tuna and other tunnids in their turn eat small *D. gigas*.

It is surprising that four papers cited in Table 4 (Erhardt *et al.* 1983, Benites 1985, footnote 1, Segura *et al.* 1996 and Wilhelm 1960, footnote 7) say that many or most stomachs were empty. Erhardt *et al.* have suggested that this may indicate a very high rate of digestion rather than any scarcity of food.

Regarding changes in the diet during the growth of *D. gigas*, Erhardt *et al.* propose that small squids eat mostly crustaceans, medium sized squids eat fish (mainly pelagic) and large squids eat squid, including the same *D. gigas*. With this classification in mind, and postponing cannibalism to be considered separately in the next section, we come to the diet of large and very large *D. gigas* eaten by sperm whales.

During the whale investigations in Chile and Perú between 1958 and 1962, the stomach contents of the specimens of *D. gigas* removed from sperm whale stomachs, were only occasionally examined when they were found to contain only squid flesh, which would indeed suggest that large *D. gigas* are only eating squids. Now it has been possible to identify these same

Table 4

The food of *Dosidicus gigas* : from stomach contents examined in the fishery.
El alimento de *Dosidicus gigas* : del contenido estomacal examinado en la pesca.

Reference	Locality	Stomach contents	Remarks
The Gulf of California Squid			
Wormuth (1976, p. 38)	Mouth of Gulf of California	<i>Hygophum atratum</i> , <i>Myctophum aurolateratum</i> , <i>Lampanyctus parvicauda</i> , <i>Diogenichthys lateratum</i> , <i>Vinciguerria lucetia</i> and <i>Benthoosema panamense</i>	Fish otoliths identified by 'Fitch personal communication'. At least two of the six species are Myctophidae, lantern fishes.
Sato (1976)	Gulf of California and west coast of Mexico 30°-22°N	'the forage...is very rich with red crabs* as the dominant component'	* <i>Pleuroncodes planipes</i> , a pelagic Anomuran
Erhardt <i>et al.</i> (1983, p. 319)	Gulf of California	Mainly sardines (<i>Sardinops sagax</i>), mackerel (<i>Scomber japonicus</i>) and red crab. During May and June the postlarvae of penaeid shrimps seem to be the favourite food. In areas of intensive fishing this squid feeds mainly on its own species* Most squids had empty stomachs or only digested material	* 'What occurs perhaps is that squid which have been badly wounded by jigs escape and, weakened, are then attacked by their own kind...It can be concluded...that this species is a very voracious predator in which high levels of cannibalism are observed when intensive fishing is performed or when no other food but squid is available'
Fusejima (1993, Table 7)	Off continental coast of Ecuador and the Galápagos Islands. 1992	November, off Ecuador: Fish 34.9%, squids 26.9%, crustaceans 9.5%, unidentified 15.6%, empty stomachs 13.1% (275 squids). December off Galápagos: Fish 65.0%, squids 23.1%, crustaceans 1.7, unidentified 3.8%, empty stomachs 6.4% (346 squids)	
The Humboldt Current Squid			
Wilhelm (1930)	Strandings in Talcahuano Bay, Chile, 36°40'S	Many sardines (<i>Sardinops sagax</i>), fragments of hake (<i>Merluccius gayi</i>), a few had small molluscs. Some had remains of <i>D. gigas</i>	'They are cannibals'
Wilhelm (1954)	The same	Hake and 'congrio' (<i>Genypterus chilensis</i>). Also four species of crustaceans, identified to genera or species. And remains of <i>D. gigas</i>	'They are cannibals, especially when in immense schools'
Fernández & Vásquez (1955)	Off Coquimbo, Chile 30°S	Of 10 stomachs more than half showed a high level of cannibalism, especially of larval forms. There were frequent remains of fish, probably <i>Trachurus murphy</i> and <i>Sardinops sagax</i>	Suggests that the diet indicates movement of <i>D. gigas</i> according to movements of the prey, and may account for its ephemeral appearances off Chile
Wilhelm (1960, unpublished; footnote 7)	Strandings in Talcahuano Bay, Chile 36°40'S	As above (Wilhelm, 1954), but adds that remains of <i>D. gigas</i> were identified from the beaks and pens, not easily digested. Many stomachs were empty	

(continued Table 4)

de Sylva (1962)	Off northern Chile	Of eight stomachs, two were empty, three contained anchovies, one a saury (garfish) <i>Scomberesox equirostrum</i> * and two contained squid flesh	* <i>Scomberesox stolatus</i> (de Buen, 1959)
Nesis (1970, p. 116)	Off Perú and Chile to 25°S, and off southern Ecuador*	Myctophids 70.2%, squids (mainly of the same species) 13.3%, plankton 7.9%, saury pike (garfish) 1.2%, ship garbage 1.2%, small fish 0.4%, unidentified 5.8% (266 squids). There were 22% of squids with empty stomachs. Showed that the rate of feeding increases with age	*We consider squids caught off southern Ecuador to be Gulf of California squids
Benites (1984)	Off Perú 07°-15°S	Mostly the stomachs were empty, but some held the remains of fish, annelid worms* and cephalopods	*Presumably free swimming polychaete worms
Benites & Valdivieso (1986)	Off all the coast of Perú	Remains of lantern fishes, crustacea, cephalopods, coelenterates and fish eggs	
Rubio & Salazar (1992)	Off Perú from 03°31'S to 12°S	30.0% of 223 males and 43.0% of 416 females contained evident remains of the same species	'A high incidence of cannibalism'
Segura <i>et al.</i> (1996)	Off Perú from 03°S to 08°S	Evident remains of the same species 15.7%, digested food 32.6%, others (?) 23.3%, fish remains 21.2% and crustacea 6.4% (343 squids). Most stomachs contained little or no food	'A high incidence of cannibalism'
R Clarke <i>et al.</i> (1978, p. 165, Table 11)	Off Chile, 28°36'S	Fish remains, probably <i>Scomberesox stolatus</i> occurred in eight or nine stomachs which contained food. One stomach had remains of a squid which was not <i>D. gigas</i> and another had squid remains, possibly <i>D. gigas</i> *	* 'This was to be expected because at Station I ₁₁ the free-living squids were seen to attack their captured fellows as the line was hauled'

squids. MR Clarke *et al.* (1976) reported on a random sample of 1,048 squid beaks collected from the stomachs of sperm whales examined in Chile and Perú between 1959 and 1961 (Fig. 3). Of these beaks only 3.60% corresponded to *D. gigas*. But R Clarke *et al.* (1988) have shown that, from a total of 8,561 flesh remains of squid from sperm whale stomachs between 1959 and 1962, *D. gigas* comprised 8,514 remains, the difference of 37 remains belonging to *Ancistrocheirus lesueuri* and *Histioteuthis* sp. Now MR Clarke *et al.*⁸ considered that all the 16 different genera of squids, comprising 18 species identified from their random sample of beaks, contributed to the diet of the sperm whale in the Southeast Pacific, whereas it is clear from the overwhelming quantity of flesh remains of *D. gigas*

that this squid, and in very minute proportion *Ancistrocheirus lesueuri* and *Histioteuthis* sp. were the only species eaten by the sperm whales, and the remaining squid species were eaten by *D. gigas* where the beaks of these species were transferred from the stomachs of *D. gigas* to the sperm whale stomachs after digestion of the squid flesh. R Clarke *et al.* (1988) have dealt with this matter at length on p. 90-94 of their report and we need not dwell further on the matter, except to give below the list of species which form the diet of large and very large Humboldt Current squids. *A. lesueuri* and *Histioteuthis* sp. were included among the squid beaks identified by MR Clarke *et al.* but we do not include them in this list because we know they are very occasionally eaten by sperm whales in the Southeast Pacific, although this is not to say that some of the beaks of these two species could not have come

⁸ One of us (O.P.) appears as a coauthor of this paper, but unfortunately she did not see the text until after publication.

from squids eaten originally by *D. gigas*, just as no doubt some of the *D. gigas* beaks could have come originally from the stomachs of this cannibalistic species.

Then large *D. gigas* from sperm whale stomachs have been eating the following squids, from MR Clarke *et al.*'s Table II: *Chiroteuthis* sp. A, *Chiroteuthis* sp. B, *Octopoteuthis* sp., *Taningia danae*, *Gonatus antarcticus*, *?Symplectoteuthis*, *Taonius megalops*, *Phasmatopsis* sp., *Mesonychoteuthis hamiltoni*, *Moroteuthis* sp., *Psychroteuthis* sp. *Oegopsids*, Species X and Y, *Vampyroteuthis infernalis*.

At least two of these genera, *Chiroteuthis* and *Gonatus*, live deep between about 700 - 1000 m (MR Clarke 1966) and so here is further evidence for ontogenetic descent in the Humboldt Current squid.

Cannibalism

Of the 15 references in Table 4 nine mention that squids found in the stomachs of *D. gigas* were mainly of this same species, although only Wilhem (1960, unpublished footnote 7) mentions that the remains were identified as *D. gigas* from the beaks and pens. Since we know from the preceding section that *D. gigas* feeds on a variety of squid species, the presence of squid flesh in the stomachs, without identification of beaks, does not necessarily mean that this squid flesh belonged to *D. gigas*. It is meanwhile very clear that *D. gigas* attacks and eats its fellows which have been caught on jigs (Duncan 1941, R Clarke *et al.* 1978, Erhardt *et al.* 1983). In this sense they are certainly cannibals, and probably they are cannibals when no other food is available, as Erhardt *et al.* have suggested.

So in spite of the general assumption (Table 4) that *D. gigas* is highly cannibalistic, it would still not be clear to what extent *D. gigas* preys on its fellows when it is not being fished and when other food is available in the form of other squid species, were it not for the unequal and changing sex ratio present from an early age and which we can only explain by predation of females upon males in this species. We shall return to this matter when discussing the sex ratio and reproduction in general.

Predators

R Clarke *et al.* (1988, p. 140) have reviewed what is known of the predators, other than the sperm whale, on *D. gigas*, but it is necessary to discuss them again here.

Of those authors who treat without discrimination the northern and southern stocks of *D. gigas*, Nesis (1970) said they were preyed upon by 'swordfish,

marlin, tuna, dolphin and apparently also blackfish' and Roper *et al.* (1984, p. 182) added, 'sharks, porpoises and other mammals'. There are more precise references to predators of the *D. gigas* stock north of the equator, what we call the Gulf of California squid. Wormuth (1976, p. 38) identified the dolphin fish *Coryphaena hippurus*, the tunny *Neothunnus macropterus* and the marlin *Makaira mitsukurii*. Blunt (1968) reported *D. gigas* from the tunnies *Thunnus albacares* and *T. obesus* in the East Pacific. A Risso's dolphin (*Grampus griseus*) shot off California had beaks of *D. gigas* in its stomach (Orr 1966). In the Southeast North Pacific (7°13'N, 90°93'W) mixed aggregations of spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*) and yellowfin tuna (*Thunnus albacares*) have been found to be feeding mostly on ommastrephid squid, probably *D. gigas*, which was positively identified from flesh remains in some stomachs (Perrin *et al.* 1973). MR Clarke (1996a) reports that in the East Pacific the dolphin called the many-toothed blackfish *Peponocephala electra* eats *D. gigas*, according to Pitman & Ballance (1992) whose paper we have not seen. Among other squids *D. gigas* is taken by the Juan Fernández fur seal (*Arctocephalus philippi*) off Chile (Torres 1987). Croxall & Prince (1996) have discussed the consumption of squids by oceanic birds, and in the Humboldt Current these squids would doubtless include juvenile *D. gigas*, whilst R Clarke *et al.* (1988, p. 110 ff) have explained how oceanic birds may feed on the heads or even complete bodies of large squids, including *D. gigas*, vomited by the sperm whale.

As R Clarke *et al.* (1988) have observed, referring to their Table 10, in the Southeast Pacific it is unlikely that the sperm whale competes directly with other predators, because the latter are probably feeding on sizes of *D. gigas* which are smaller than those eaten by all but the smallest sperm whales. This is obvious from Fig. 2 but would appear to be contradicted by MR Clarke's statement (1982-1983) that the average weight among all squid eaten by sperm whales is 1.3 kg off Western South America, that is to say, in the Humboldt Current. His estimate came from the sizes and species of beaks collected from the stomachs of sperm whales in Chile and Perú (MR Clarke *et al.* 1976); but R Clarke *et al.* (1988, p. 90-94, p. 99) have explained how this unacceptable estimate came about, and we have already referred to the matter in the present report. As much may be said for the mean wet weight of about 11 kg estimated for *D. gigas* as prey from the beak collection examined by MR Clarke *et al.*, which again is explained by R Clarke *et al.* On their page 99, they gave the average estimated weights of *D. gigas* examined from the stomachs: these were 17.5 kg from female sperm whales, 17.2 kg from small males less than 12 m in length, and 25.7 kg from large males. The smallest

sperm whales taken, 6.0-6.9 m in length, were eating *D. gigas* of average weight 4.6 kg from male whales, and one squid of 10.3 kg from a female whale (R Clarke *et al.* 1988, Table 14). See also Fig. 3. Clearly, MR Clarke (1996 a, p. 1059) was mistaken when, referring to the sizes of squids in the diet of sperm whales, he observed 'The mean weights eaten are greatest in the Antarctic (7.2 kg)'.

We have briefly explained in the Introduction how R Clarke *et al.* (1988) estimated the enormous annual consumption of *D. gigas* by the sperm whale population in the Humboldt Current between 1959 and 1962, and how this prompted them to propose a large-scale exploitation of *D. gigas* which led to the present multinational fishery for this squid off Chile and Perú. For more details the reader is invited to consult their report. Meanwhile the present fishery off Chile and Perú has joined the known predators of *D. gigas* and we shall see that during 1989-92 off Perú 25.6% of this squid in the catch were sexually immature, whereas during 1959-62 the *D. gigas* eaten by sperm whales comprised only 0.21% immature and nearly all the squid eaten had reproduced at least once. We shall have more to say on this difference when the exploitation of *D. gigas* is discussed.

Parasites

Severino *et al.* (1993)⁹ and González & Mendo (in press) have reported on the parasites identified from *D. gigas* fished by, respectively, Japanese and Korean vessels off the north coast of Perú. González & Mendo refer to Russian authors writing on parasites in *D. gigas* from other parts of the Southeast Pacific.

Severino *et al.* and González & Mendo obtained similar results, although the latter authors reported in more detail, considering the incidence of parasitism according to the size, sex and sexual condition of the host. Both papers report larvae of the nematode *Anisakis* sp. and plerocercoid larvae of the cestode *Tentacularia* sp. in the intestine, the mantle and the surface of the gonads of *D. gigas*. Of 205 squids examined by Severino *et al.* virtually all (99.02%) were parasitized by *Anisakis* sp. or by *Tentacularia* or by both. González & Mendo found a rather smaller proportion parasitized (73.85%) in the 260 squids which they examined.

Adult nematode worms of the genus *Anisakis* are found in the stomachs of all sperm whales in all parts of the world, sometimes in very great quantities (Fig. 3).

Anisakis is a nematode difficult to identify as to species, and Severino *et al.* and González & Mendo give only *Anisakis* sp. from the Humboldt Current squid, whereas Delyamure & Skryabin (1971), in their review of the helminth parasites of the sperm whale, list seven species of *Anisakis* from different oceans of the world. But, during the whale investigations conducted in Chile and Perú between 1958 and 1962, samples of *Anisakis* were collected on nine occasions from sperm whale carcasses at Iquique and Talcahuano in Chile and at Paita and Pisco in Perú. These samples were identified in the British Museum (Natural History) in London; eight samples were of *Anisakis physeteris* Baylis, 1923 and the ninth was *Anisakis simplex* (Rudolphi 1809), a species more slender in body than *physeteris*. Then the Humboldt Current squid is a primary host of *A. physeteris* and probably of *A. simplex*, and the sperm whale is a secondary host of these nematodes, at least in the Southeast Pacific, because, speaking only of *A. physeteris*, this species is known from sperm whales in many other oceans, and many other species of squids, prey of sperm whales in these oceans, must carry larval *A. physeteris*. The squids must be re-infected when the adult nematodes, including gravid females, are vomited together with squid beaks, a process which R Clarke *et al.* (1988, p. 138) have estimated to take place, in the Southeast Pacific, every 5-6.3 days in male sperm whales and every 7-8.4 days in females.

Severino *et al.* and González & Mendo have called attention to 'human anisakiasis' due to eating raw squids and fish (presumably as 'cebiche') in Perú. Deadorff & Overstreet (1991) have discussed the symptoms produced.

The plerocercoid larvae of the cestode '*Tentacularia* sp. (*Trypanorhyncha*)', found by Severino *et al.* and González & Mendo in *D. gigas*, may also have a secondary host in the sperm whale in the Southeast Pacific, because Delyamure & Skryabin, p. 282 give *Trypanorhyncha* sp. as larvae attached to the stomach wall in sperm whales and other marine mammals from the Kurile Islands.

At the First Congress on Zoology in Chile at Santiago de Chile in September 1960 the late Dr Ottmar Wilhelm told the first author that some of the *D. gigas* stranded in Talcahuano were parasitized by the tapeworm *Bothriotaenia* sp. To our knowledge the genus *Bothriotaenia* has previously been reported from fish (Benham 1901, p. 116) and from birds (Borradaile *et al.* 1935, p. 230), so that *D. gigas* is a new host for this cestode. *Bothriotaenia* has not yet been reported from sperm whales of the Southeast Pacific, where the only tapeworm reported so far from these whales is *Tetraphobius affinis* (Loeffer 1891) which has not yet been identified in the Humboldt Current squid. It

⁹ Severino R, E Morales, I Espinoza, A Soko, P Zubiate & D Florindez. 1993. Parasitos de *Dosidicus gigas* 'Pota' del Mar Peruano. III Reunión Científica, Instituto de Ciencias Biológicas 'Antonio Raimondi', UNMSM, diciembre de 1993. Libro de Resúmenes, p. 95.

does appear that there is still scope for work on the parasites of *D. gigas*.

Sexual maturity

Results by previous workers on the attainment of sexual maturity in *D. gigas* are summarised in Table 5. Two papers do not give the mantle lengths at sexual maturity, but the mantle lengths estimated according to sex in five citations are not much different from each other. R Clarke *et al.* (1978) gave comparatively higher values for both males and females, but here only 13 squids were involved, and Masuda *et al.* (1998) proposed two length groups of early and late maturing squids.

We can make no estimates on maturity for the present material from the fishery but Tafur & Rabi (1997) obtained mean values for the mantle lengths, plotting a curve of increasing percentages sexually mature against increasing mantle lengths, and then taking the lengths at which 50% of males and 50% of females were sexually mature. We therefore accept these as the best estimates. To the nearest centimetre they are 29 cm for the mantle length in males and 32 cm for that in females.

In Table 6 these mantle lengths at sexual maturity are applied to the present data from the fishery by months and years between 1989 and 1992. We can see no trend in the percentages of immature squids, either during the course of a year or from year to year. For example, in the fishery of March and April in 1990 all, or virtually all, of the squids of both sexes were immature, whereas in 1992 in March 57.6% of males and 63.1% of females were immature, and in April 4.1% of males and 10.1% of females were immature. We are unable to attribute these apparently haphazard results to changes in distribution or to the effects of fishing, but rather believe they are probably due to changes in the sizes of the hooks on the jigs employed during a fishing season, according to the sizes of squids available at any fishing station or to the sizes preferred by the market at any one time. Segura *et al.* (1996) have noted that jigs of many different sizes are used in this fishery.

Among the squids from the fishery for the whole period 1989-92 there was no great difference between the sexes in the proportions immature, being 21.8% among 9,475 males and 26.7% among 33,781 females. For comparison with the unsexed samples from sperm whale stomachs, we may say that in the total catch of 43,256 squids there were 25.6% sexually immature. But among the 4,872 *D. gigas* recovered from sperm whale stomachs, between 1959 and 1962, there were only 10 squids of mantle length less than 32 cm, that is to say, only 0.21% were immature. Then we may conclude that

virtually all *D. gigas* eaten by sperm whales are sexually mature.

Sex ratio

It will be recalled that squids removed from sperm whale stomachs in 1959-62 were not sexed, so that this section refers only to squids from the fishery.

A considerable excess of female *D. gigas* may be seen at once in Table 2 where the sex ratios per voyage off Perú between 1989 and 1992 varied between 1:1.36 and 1:9.13, a range depending, as will be seen, largely on cannibalism at different times of the year.

We assume that at spawning as many males are produced as females, and we see in Fig. 6, showing the percentages of males and females at each 2 cm increment in mantle length, that at 13 cm mantle length the sex ratio is still 1:1, that is, 50% of each sex. Thereafter the excess of females begins and we can only attribute this to cannibalism of the males by the larger females.

We have accepted Tafur & Rabi's estimate (1997) for the onset of sexual maturity in *D. gigas* as 29 cm mantle length for males and 32 cm for females: it can hardly be a coincidence that in Fig. 6 the proportion of males completes its first decrease at 33 cm mantle length and the proportion of females, a mirror image of the males, completes its first increase also at 33 cm. This is also reflected in the sex ratios for the whole period 1989-1992 at the foot of Table 7, plotted also in Fig. 6, where there is an abrupt rise in the female component from 1:3.80 in the group of female mantle lengths 21-30 cm to 1:5.32 in the group of 31-40 cm mantle lengths. We propose that this group is in the first sexual season with intense copulation followed by cannibalism of the males by the females post-copulation. Thereafter as may be seen in Fig. 6, Table 7 and Fig. 7 there is a period of growth, between 41 cm and approaching 90 cm mantle length, when the sex ratio stays fairly constant around 1:3, when there is relatively little cannibalism and both sexes are free feeding. This may also be seen in Fig. 4. At 85 cm mantle length there is a second abrupt increase in the proportion of females (Fig. 6) and the sex ratio in the 91-100 cm group rises to its highest point for females 1:9.07 (Table 7, Fig. 7). We believe this to be the second sexual season, with intense copulation and post-copulatory cannibalism of the males. In the last group 101-105 cm, only the females remain alive for a time.

We now examine in Fig. 8 the sex ratio by months of the year for *D. gigas* fished off Perú between 1989-92. There are two pronounced peaks for females, at sex

Table 5

Results on sexual maturity, including estimates of the mantle length, in male and female *Dosidicus gigas* from the fishery.Resultados sobre la madurez sexual, incluyendo estimados de la longitud del manto en *Dosidicus gigas* machos y hembras de la pesca.

Reference	Location	Sample size	Mantle length at sexual maturity		Remarks	
			Males	Females		
Nesis (1970, p. 113, Fig. 4)	Off coasts of Chile, Ecuador and Perú	274. Numbers by sex not recorded	Most at less than 20-25 cm. All mature above 29-30	Some more than 36-37 cm. Nearly all mature by 40 cm	Employed three stages of maturity in males and four in females. At several stations east of the Perú-Chile Trench numbers of males up to 43 cm and females up to 44 cm were still immature. Nesis believed that the cold water had delayed development	
R Clarke <i>et al.</i> (1978, p. 165, Table 11)	Off coast of Chile	6 males, 7 females	52 cm	Still immature at 59 cm	Maturity determined by Dr P. García-Tello	
Erhardt <i>et al.</i> (1983, p. 319-20)	Gulf of California and adjacent waters	Males. Numbers not given Females 1631	18-25 cm (2-3 months old)	35-40 cm (4-6 months old)	"Size at first maturity is dependant on food availability and temperature...."	
Benites (1984, p. 11)	Off coast of Perú	540. Numbers by sex not recorded	18-23 cm when 35% were mature	23-27 cm		
Rubio & Salazar (1992, p. 7-8)	Off coast of Perú	223 males 404 females			The stages of maturity according to Nesis (1970) were employed. 90.1% of males and 41.8% of females were completely mature, but mantle lengths are not mentioned	
Fusejima (1993, p. 10, Fig. 21)	Off coast of Ecuador and around Galápagos Is.		22-25 cm	20-30 cm	In December some females larger than 30 cm were still immature	
Segura <i>et al.</i> (1996, p. 36, Fig. 20)	Off coast of Perú	447. Numbers by sex not recorded but, the context shows that all were females			No mantle lengths mentioned. 23.7% of the sample were immature	
Tafur & Rabi (1997, Table 1 Figs 1 and 2)	Off coast of Perú	Totals not recorded but samples of 10 males and 10 females taken for analysis on each fishing trip from 8,876 males and 8,807 females	28.8 cm	32.2 cm	Employed stages of maturity (Table 1) modified from Nesis (1970). Mean mantle length at maturity when 50% of males (Fig. 2) and of females (Fig. 1) were mature	
Masuda <i>et al.</i> (1998)	Off coast of Perú	Apparently males and females	203 376	Observed two groups where all squids were mature at 1. 20-30 cm 2. 50-60 cm	30-40 cm 65-75 cm	See text

Table 6

Percentages of sexually immature squids among male and female *Dosidicus gigas* fished off Perú between 1989 and 1992.

Porcentajes de calamares sexualmente inmaduros entre *Dosidicus gigas* machos y hembras pescados frente al Perú entre 1989 y 1992.

Months	Percentages sexually immature										Numbers of squids	
	Years										Males	Females
	1989		1990		1991		1992		1989-1992			
♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀			
January							0.0	0.0	0.0	0.0	248	771
February							0.0	0.5	0.0	0.5	478	1,502
March			100	100			57.6	63.1	72.8	68.8	728	2,172
April			100	100			4.1	10.1	40.5	26.1	980	3,010
May							13.2	23.4	13.2	23.4	524	2,466
June							20.6	27.9	20.6	27.9	722	3,168
July			70.8	75.9			9.1	19.2	27.7	43.3	1,064	3,886
August			59.3	66.0			23.9	23.9	30.2	36.9	1,597	4,869
September							16.4	24.1	16.4	24.1	525	2,009
October					4.9	9.7			4.9	9.7	1,277	3,808
November	3.8	13.7			1.5	4.5			2.2	8.8	733	3,191
December	13.8	35.6			2.2	5.4			4.8	22.8	599	2,929
Jan-Dec	7.7	25.3	84.0	77.3	3.6	7.6	17.3	23.2	21.8	26.7	9,475	33,781
Numbers of squids	349	3,185	1,154	4,015	2,260	6,743	5,712	9,838	9,475	33,781	Total squids 43,256 [#]	

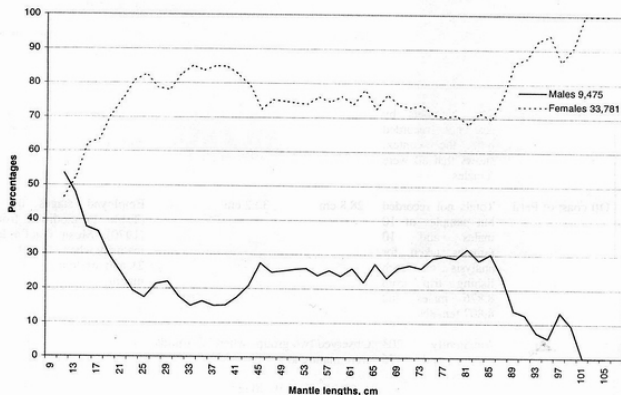


Figure 6

Percentages of males and females at each 2 cm increment in mantle length of *Dosidicus gigas* from the squid fishery off Perú between 1989 and 1992.

Porcentajes de machos y de hembras a cada incremento de 2 cm de la longitud del manto en *Dosidicus gigas* de la pesca de calamares frente al Perú entre 1989 y 1992.

Table 7

Sex ratios at each 10 cm increment in mantle length for *Dosidicus gigas* fished off Perú between 1989 and 1992.Relación de sexos a cada 10 cm de incremento de longitud del manto para *Dosidicus gigas* pescados frente al Perú entre 1989 y 1992.

	Mantle length, cm										Total
	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	
1989											
Shinko											
Maru 2											
05 Nov-15 Dec											
Male		27	274	48							
Female		481	2,419	285							349
Sex ratio		1:17.8	1:8.8	1:5.9							3,185 1:9.1
1990											
Nansen											
25 Mar-06 April											
Male	463	170	0								
Female	560	297	4								633
Sex ratio	1:1.2	1:1.18									861 1:1.4
Kwan Yang 108											
01 Jul-24 Aug											
Male	66	270	114	67	4	0					
Female	261	1,747	903	213	29	1					521
Sex ratio	1:4.0	1:6.5	1:7.9	1:3.2	1:7.3						3,154 1:6.1
1991											
Japanese vessels											
01 Oct-14 Nov											
Male		16	460	426	103	1					
Female		56	668	1,134	465	7					1,006
Sex ratio		1:3.5	1:3.6	1:2.7	1:4.5	1:7.0					3,330 1:3.3
Korean vessels											
15 Oct-31 Dec											
Male		65	269	410	406	82	20	2			
Female		200	853	1,033	989	281	50	7			1,254
Sex ratio		1:3.1	1:3.2	1:2.5	1:2.4	1:3.4	1:2.5	1:3.5			3,413 1:2.7
1992											
Japanese vessels											
09 Apr-14 Sep											
Male	1	703	858	74	16	101	225	383	15	0	2,376
Female	2	1,886	4,871	791	134	219	549	978	335	7	9,772
Sex ratio	1:2.0	1:2.7	1:5.7	1:10.7	1:8.4	1:2.2	1:2.4	1:2.6	1:22.3		14.2
Korean vessels											
14 Jan-12 Sep											
Male	35	248	139	85	287	857	1,103	536	46	0	3,336
Female	153	1,035	533	316	829	633	846	1,493	218	10	10,066
Sex ratio	1:4.4	1:4.2	1:3.8	1:3.7	1:2.9	1:3.1	1:2.6	1:2.8	1:4.7		1:3.0
1989-1992											
All vessels											
Male	565	1,499	2,114	1,110	816	1,041	1,348	921	61	0	9,475
Female	976	5,702	1,251	772	446	3,141	3,445	2,478	553	17	33,781
Sex ratio	1:1.7	1:3.8	1:5.3	1:3.4	1:3.0	1:3.0	1:2.6	1:2.7	1:9.1		1:3.6

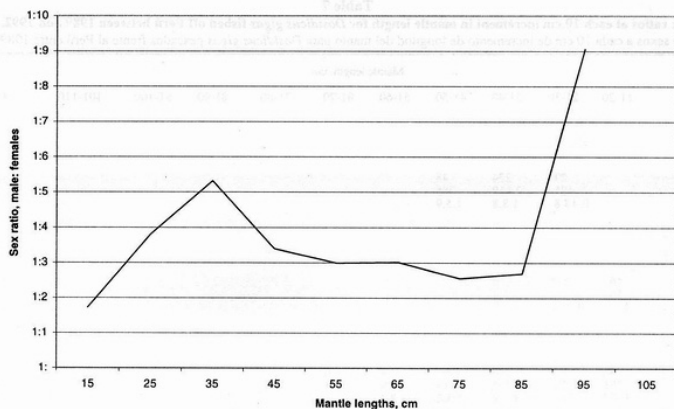


Figure 7

Sex ratios at 10 cm increments of mantle length for *Dosidicus gigas* fished off Perú between 1989 and 1992.

Relación de sexos en incrementos de 10 cm de la longitud del manto en *Dosidicus gigas* pescado frente al Perú entre 1989 y 1992.

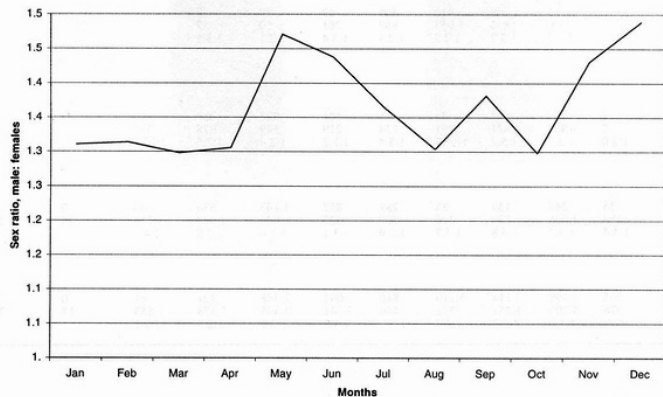


Figure 8

Monthly sex ratios in *Dosidicus gigas* fished off Perú between 1989 and 1992.

Relación de sexos por meses en *Dosidicus gigas* pescado frente al Perú entre 1989 y 1992.

ratios 1:4.71 in May and 1:4.89 in December. We propose that these are the months of intense copulation and post-copulatory cannibalism of the males by the females.

With this interpretation of the varying sex ratio, and with information from squids from sperm whale stomachs as well as from the fishery, we may now attempt the elucidation of the sexual cycle in *Dosidicus gigas*.

Sexual cycle and longevity

Reviewing previous work on the sexual cycle and longevity of *D. gigas* suggests that no very convincing proposals have emerged up to now. Perhaps Tafur & Rabi (1997) have produced the likeliest arguments, but no authors have combined information from the fishery with that from the larger squids from sperm whale stomachs, something which we shall attempt after the following paragraph on previous work.

MR Clarke (1980, p. 301; 1982-83, p. 156) found that in several fast growing squids growth could occupy one or two years, but in 1982-83 he went on to say that in nearly all squids the females die at spawning. This cannot be the case with *D. gigas* because of the considerable excess of females in all but the smallest animals: the overall sex ratio in the fishery off Perú in March 1984 was 1: 7.1 (Benites 1985, footnote 1) and in November-December 1989 the ratio was 1:7.3 (Rubio & Salazar 1992) whilst we have found that between 1989 and 1992 in the same fishery off Perú the overall ratio was 1: 3.57 (Table 2). In mass strandings of *D. gigas* at Talcahuano in Chile, Wilhelm (1930, 1954; 1960, unpublished, footnote 7) found that all the females examined between the end of March and the beginning of May had spent ovaries. Erhardt *et al.* (1983, p. 326) found that in the Gulf of California stock of *D. gigas* (which we believe to be separate) there was a high percentage of spent females in May-June, corresponding to our spawning peak in December in the Southern hemisphere. They proposed that the Gulf of California stock has multi-cohort components and that the squids live to a maximum of 16-20 months. Nesis (1970) noticed that in the fishery off Chile and Perú there was a reduction in the number of males at sexual maturity, just as we also have observed off Perú (Fig. 6). Nesis went on to say 'Evidently this phenomenon is the result of earlier death of the males, which reach sexual maturity earlier than the females and die after the first spawning at an earlier age'. He found three size groups in the catches which he considered to be one year old at 20-25 cm mantle length, two years old at 30-35 cm, and the larger squids 3-4 years old. He considered that most males mature at one year old and most females at two years old. Benites & Valdivieso (1986) found at least

three cohorts of *D. gigas* but did not say whether these corresponded to yearly age groups. Rubio & Salazar (1992) found that 84.4% of females were copulating during November-December 1989. Since spawning follows immediately on copulation, this is similar to the results of Yamashiro *et al.* (1995, Fig. 4; footnote 5), who found that spawning mainly in winter and spring is at a peak in November. Tafur & Rabi (1997) examined 8,807 females and 8,876 males collected from the Perú fishery between 1991 and 1994. Spawning peaks were identified by three different methods - the spawning progression, the variation in nidamental gland length with mantle length (the most acceptable method) and the gonado-somatic index: (Gonad weight $\times 10^8$ / mantle length³). They found that spawning in *D. gigas* occurs during all the year, the largest peak during October-January and highest in November, which agrees with the results of Yamashiro *et al.* (1995; footnote 5). Tafur & Rabi also noticed secondary peaks in the winter, in July and August. They considered that *D. gigas* experiences two spawning periods during its lifetime, and they suggested two possible explanations: either there are two spawning periods in the same population, or there are two populations mixed in the same fishing area, one a small-sized early maturing population and the other a larger-sized late maturing population. Nesis (1970) had noticed something similar and recently Masuda *et al.* (1988) have investigated this matter and have concluded that '*D. gigas* consists of early and late maturing groups' (Table 5). We shall return to this when we have elucidated the spawning seasons.

Turning now to the present material we are largely concerned with *D. gigas* from sperm whale stomachs although none of these animals were sexed. At Pisco in 1962 the mantles were measured and weighed from 777 squids during all months of that year. We use here a 'Condition Index' for comparing Mantle Weight with Mantle Length by taking the means of the logarithms of mantle weight and mantle length in each month, converting these means to common numbers and then dividing the value for mantle weight by that for mantle length to give the condition index. The monthly indices are plotted in Fig. 9.

The figure shows two strong peaks in April and November when the squids are heaviest. Our interpretation is that in these two months the mature females are heavy with ripe eggs and the males also are ready with their spermatophores. In the following months, May and December, copulation takes place, the spermatophores open to release the sperms which fertilise the eggs as the females expel them; the females are spawning. Our results from the varying sex ratio in the catch support this interpretation, for the excess of females over males was greatest in May and December

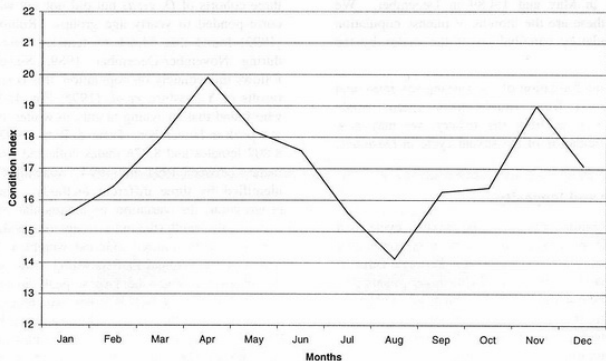


Figure 9

Monthly condition index for 777 specimens of *D. gigas* examined from sperm whale stomachs at Pisco in 1962.

Índice de condición mensual en 777 especímenes de *Dosidicus gigas* examinados de los estómagos de cachalotes en Pisco en 1962.

(Fig. 8), which we have attributed to post-copulatory cannibalism of the males by the females. Other authors, like Rubio & Salazar (1992), Yamashiro *et al.* (1995, footnote 5) and Tafur & Rabi (1997), have obtained results not unlike ours on the spawning peak or peaks in *D. gigas*. None of these authors mention the spawning peak we designate in May, but at Talcahuano in Chile Wilhelm (1930, 1954; 1960 unpublished, footnote 7) found that all females examined between the end of March and the beginning of May had spent ovaries. Wilhelm did not mention spawning around December but his material came from the great strandings of *D. gigas* which take place at Talcahuano only at the end of summer. Then off Pisco there are two spawnings of *D. gigas* and we believe that this is so in the Humboldt Current to the north and to the south of Pisco, except that to the south, around Talcahuano, spawning may begin about a month earlier than off Pisco. Tafur & Rabi (1997) consider that some spawning occurs in all months, and this may be so to a minor extent, and perhaps the minor peak in September for the sex ratio in Fig. 8 and the step in September in the condition index (Fig. 9) may suggest subsidiary spawning, but we are here concerned with the two major peaks for maturation of the eggs in April and November followed by copulation and spawning in May and December. We therefore support the first of Tafur & Rabi's possibilities (1987), that there are two spawning periods in the same population.

Before we can trace the life history we must refer to methods of age determination using the statoliths and *gladii* (pens) of squid, introduced since 1978. In the present report we cannot apply these methods directly because only data and no biological material are available to us. But Arkhipin & Murzor (1986) have described the statoliths in *D. gigas* and Masuda *et al.* (1996) have used statoliths to examine age in some *D. gigas* taken off Perú. We have not seen these two papers, but recently Masuda *et al.* (1998) have examined the statoliths from 584 specimens of *D. gigas* mostly taken off Perú. Under the microscope the statoliths show increments in their structure which are considered to be daily increments. Masuda *et al.* found that the maximum estimated ages were 352 days for a male with mantle length 77 cm and 338 days for a female with mantle length 86 cm. Masuda *et al.* therefore suggested that the life span could be one year. We cannot accept this because our material includes much larger squids, but we can apply their results, which indicate that, assuming a constant grow rate, *D. gigas* males grow at 6.6 cm per month and females at 7.6 cm per month.

Turning now to the life history, the *D. gigas* recently sexually mature spawn for the first time in May or in December. We choose for the moment May. These are the group with mantle lengths 31–40 cm (Table 7, Figs 6 and 7). Five months have elapsed since they were spawned in the previous December. During these five months, applying the results of Masuda *et al.*, the males

will have grown to mantle length 33.0 cm and the females to 38.0 cm, which are lengths within the group 31-40 cm. However, seven months elapse before squids spawned in May reach their first spawning season in December, during which they will have grown, at the same growth rates, to 46 cm mantle length for males and 53 cm for females, that is, they will have grown larger than the mean sizes at sexual maturity. Now there seems no reason to suppose that there is less food available in winter making growth slower during the winter months (May-December) than in the summer months (December-May), although this may in fact happen; we recall Erhardt *et al.*'s observation (1983) that 'Size at first maturity is dependant on food availability and temperature' (Table 5). With constant growth rates we can only assume that squids spawned in May mature after seven months, to spawn in the sexual season in December, when they will have grown to 46 and 53 cm mantle length in males and females respectively (Fig. 10). Here then are the 'early maturing' and 'late maturing' groups of Tafur & Rabi and Masuda *et al.*, although we see no reason to invoke two separate populations.

The spawning is summarized in Fig. 10, always assuming constant rates of growth. Squids spawned in May and December achieve a second spawning season when they are grown to the same sizes, 79 cm and 91 cm mantle length in males and females respectively. These are the groups represented as 85-100 cm in Fig. 6 and the ranges are fairly close. Small variations in the two growth rates could bring 79-91 cm up to 85-100 cm. To our mind there can be no third spawning season because after five months from the second spawning season for squids spawned in December, and more so for those spawned in May after seven months, both males and females will be dead, since males grow to no more than 100 cm mantle length (Fig. 6) and females to no more than 120 cm.

The few males which live to the maximum mantle length of 100 cm will have grown from 79 cm at the time of the second spawning, and this takes three months with the rate of growth unchanged. So the maximum life span or longevity in males is 15 months. Similarly, it takes four months for females growing from 91 cm mantle length to a maximum of 120 cm, giving a longevity of 16 months.

Concluding this chapter on breeding and the life cycle we are pleased to quote a welcome observation by an anonymous referee:

'Also biological seasons (cycles) obviously are controlled not by the calendar but by the environment. Year to year shifts are to be expected, as well as El Niño effects and possibly global warming'.

Allometric growth

From their weight/length equations Erhardt *et al.* (1983, p. 325) and Rubio & Salazar (1983, p. 7) proposed, respectively for the Gulf of California squid and for the Humboldt Current squid, that growth may be isometric in *D. gigas* because of the similarity between the regression coefficients for parts of the body (Table 3). The equivalent regressions in Table 3 for squids from sperm whale stomachs do not support isometric growth, although it is seen that the mean of the coefficients for mantle weight, 2.01, and for head-and-arms weight, 1.65, emerges as precisely the coefficient for total weight, 1.83. So the mantle, doubtless because of the sexual cycle, is increasing comparatively in weight more than the head-and-arms as the animal grows in size.

But when weight is omitted and we consider only morphometry, we cannot again confirm isometric growth in *D. gigas*. At Pisco in 1962, 102 complete squids from sperm whale stomachs were measured for standard length, mantle length and head-and-arms length. The standard lengths ranged from 0.88 to 1.79 m. Huxley's formula (1932) for simple allometry, $y = bx^h$, was applied in its logarithmic form, $\log y = \log h + \infty \log x$ where x was the standard length, y was either the mantle length or the head-and-arms length, all in metres, ∞ the growth coefficient and h a constant. The results are shown in Table 8:

Table 8
Allometric growth in the Humboldt Current squid.
Crecimiento alométrico en el calamar de la Corriente de Humboldt.

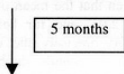
	Mantle length (m)	Head-and-arms length (m)
Growth coefficient (∞)	0.8358	1.1969
Constant (b)	1.2859	-0.7921
Correlation coefficient	0.8600	0.8680

Head-and-arms were growing faster ($\infty = 1.20$) than the mantle ($\infty = 0.84$). The squids were not sexed, but the female *D. gigas* is only slightly larger than the male and this need not affect the relative proportions of mantle and head-and-arms. Then in both sexes growth is not isometric.

The shift to larger sizes of prey as the squid grows explains the faster growth of the head-and-arms (brachial crown), an aspect of squid ontogeny which is discussed by Rodhouse & Nigmatullin (1996).

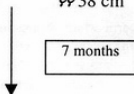
FIRST SPAWNING SEASON IN MAY:

Spawned in December



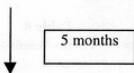
First spawning in May

♂♂ 33 cm ♀♀ 38 cm



Second spawning in December

♂♂ 79 cm ♀♀ 91 cm



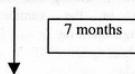
Third spawning in May

(♂♂ 112 cm) (♀♀ 124 cm)

Theoretical, see text

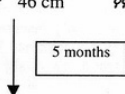
FIRST SPAWNING SEASON IN DECEMBER:

Spawned in May



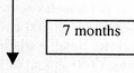
First spawning in December

♂♂ 46 cm ♀♀ 53 cm



Second spawning in May

♂♂ 79 cm ♀♀ 91 cm



Third spawning in December

(♂♂ 125 cm) (♀♀ 137 cm)

Theoretical, see text

Figure 10

Sexual cycles in the Humboldt Current squid.

Ciclos sexuales en el calamar de la Corriente de Humboldt.

Growth increments

Nesis (1970, p. 115) considered that for *D. gigas* in the Humboldt Current the average monthly growth increment in the first year was 2-2.5 cm and during the second year, 1-1.2 cm. Erhardt *et al.* (1983, p. 325) found higher growth rates for the Gulf of California population of this squid. They presented monthly increments in mantle length for the five cohorts they recognised. In cohort 1 there were animals of age 1-4 months growing at 9 cm per month and those of 7-10 months were growing at 1-2 cm per month; however, in cohort 2 squids aged 7-8 months were growing at 5 cm per month. Benites (1985, footnote 1) commented on the results of Erhardt *et al.* and considered that off Perú a *D. gigas* one year old would have reached a size (presumably mantle length) of about 60 cm. Benites considered that *D. gigas* grows much more rapidly than other oceanic ommastrephids.

So far as we are aware none of these authors derived their increments from statoliths. In the previous section we have assumed constant growth rates of 6.6 cm and 7.6 cm per month respectively in male and female *D. gigas*, derived from Masuda *et al.*'s work on statoliths (1998). During ontogeny there may well be changes in the growth rates but we cannot elucidate these from our data. Nonetheless constant growth rates fit well enough with our spawning peaks in May and December and the sizes of the squids at these times, giving us confidence in our results. This voracious animal grows very fast, indeed even faster than Benites (1985) believed.

Migrations

Kuroiwa (1998) has examined the catch of *D. gigas* per unit of effort at numerous fishing stations off the coasts of Ecuador and Perú in different months of the year, but he comes to no conclusions on migration: he says 'the mechanism affecting formation of good fishing grounds has not been clarified'.

Nesis (1970) had proposals for the migrations of *D. gigas* in the Humboldt Current. He observed the largest numbers of this squid from the equator to 18°S, an extensive zone where apparently he considered that most spawning takes place because he only found larvae smaller than 3 mm north of 20°S. He said that the young squid scatter over a vast area and follow the Current mostly northward and westward. As they get older Nesis considered that they begin to move southeast and east to the coastal waters of southern Perú, northern Chile and central Chile, particularly off Talcahuano, the main migration taking place in the summer and autumn. Here, close to the coast, the squids are feeding heavily and vast numbers are stranded whilst chasing schools of fish or poisoned by excessive phytoplankton blooms ('aguaje'). Nesis had in mind

Wilhelm's observations (1930, 1954) on the strandings of *D. gigas* at Talcahuano, although Wilhelm considered that the squid which stranded had been chasing fish rather than poisoned by an 'aguaje'; Gunther (1936, p. 234) was also of the opinion that these strandings had a 'biological rather than a hydrological cause'. Nesis completes his account saying that the squid which are still alive move northwest and west, gradually maturing, and finish their lives over deep water on the spawning grounds off northern and central Perú. He believed that a 'considerable proportion of the squid die after the first spawning'. Nesis' proposal certainly fits in with Mariátegui & Taipe's general observation (1996) that off northern Perú *D. gigas* is most abundant in winter and spring and least abundant in summer and autumn.

Now R Clarke *et al.* (1988, p. 72 ff) have shown that sperm whales increase in fatness from north to south in the Southeast Pacific, that is, 'from Paita to Pisco to Iquique and (where sufficient data were available) to Talcahuano'. Since *D. gigas* is virtually the only food of the sperm whale in the Humboldt Current, they attributed this increase in fatness to an increasing abundance of *D. gigas* from Perú southwards to Chile. They went on to say,

'There is already evidence for the special abundance of *D. gigas* off Chilean coasts. D'Orbigny (1835-43) described the sea as covered with this squid in late summer in 33°S (near Valparaíso) and records great strandings in 23°S at Cobija (north of Antofagasta) and at Arica (18°30'S).'

They go on to mention the strandings in Talcahuano Bay (36°40'S) between February and April to which we have already referred. Continuing, they say

'Strandings have also been reported in the Gulf of Arauco in 37°15'S (Wilhelm, 1930) and lesser ones at many points on the coast, from Chiloé (42°-43°S) to Caldera (27°S) and further north (Wilhelm, 1954), whilst great concentrations have been observed at sea in summer between 40 and 100 miles off the littoral of the province of Concepción (36°20'S - 37°10'S) and especially off Isla Santa María (37°S) (Wilhelm 1960, unpublished).

These records extend along most of the coast of Chile, from 18°30'S to 43°S, a latitude which, according to Gunther (1936) is near the southern boundary of the Humboldt Current,.....'

In Perú, on the other hand, these authors found only one reference to a stranding of squids: Schweigger (1947, p. 157) saw great numbers of squids, '50-80 cm long' stranded on beaches south of Lima; he called them *Sepia*, although the '*Sepia*' shown in his Fig. 20 is not a cuttlefish but a squid, although the fins appear to extend too far forward for it to be *D. gigas*.

Over against this evidence for abundance off Chile, R Clarke *et al.* explain how, between August and November 1968, Nesis (1970) caught most *D. gigas* off Perú as far as 18°S. But they go on to say 'Possibly migration is involved here, because the strandings and sea surface concentrations in Chile are nearly all coastal phenomena in summer, whereas Nesis' observations were made in late winter and early spring and mostly far from the coast.'

Once again, then, there is support for Nesis' proposals, although it must not be supposed that spawning only takes place between the equator and 18°S. Wilhelm (1960, unpublished; footnote 7) admitted that the spawning banks off Chile were unknown, but he had encountered on various occasions young examples of *D. gigas* south of Isla Santa María. Also, although Nesis speaks of 'an annual mass migration' (our italics) from whales off northern Perú southward and towards the coast in summer, this is not a general exodus, because Fig. 11 shows that sperm whales off Paita (05°09'S) take *D. gigas* of moderate and large size in all months of the year.

This Fig. 11 shows the percentages of mantle lengths at 10 cm intervals of *D. gigas* measured from sperm whale stomachs in each month of the year at the whaling stations at Paita (05°09'S) in 1959-61, Pisco (13°46'S) in 1960-62, Iquique (20°15'S) in 1960 and Talcahuano (36°40'S) in 1961. Fig. 11 needs to be studied with caution because it obviously does not represent the monthly size distribution of *D. gigas* in the sea; sperm whales go for the larger squids, so that the smallest squids in Fig. 11, of 30-40 cm which are spawning in May, are severely under-estimated. Further, the sperm whales were mostly caught between 40 and 150 miles from the coast so Fig. 11 tells us nothing about the squids nearing the coast or departing from it. However, something can be gleaned from the figure.

The smallest group of *D. gigas* eaten by sperm whales is 30-40 cm mantle length except for a 20-30 cm group which appears only at Talcahuano in March. We first consider this 30-40 cm group which spawns for the first time in May and also the late spawning group of 46-53 cm mantle length - say 40-50 cm - which spawns for the first time in December. The 30-40 cm group occurs in April at Talcahuano, but not in its spawning month of May. However we have suggested that spawning may take place about a month earlier off Talcahuano and the very small group of 20-30 cm may be associated with this earlier spawning. It is unfortunate that observations at Talcahuano were only made between March and June. The group only appears once more, at Iquique in December, which is not the spawning month for the group. At Pisco and Paita it is absent except for an indication in April at Pisco. The late spawning group, 40-50 cm mantle length, is absent from Talcahuano

between March and June but appears at Iquique in April, May, June and October, but not in its spawning month of December. At Pisco it appears in March and August, although there is a minimal presence in April, September, October and December. In Paita it is absent throughout the year. We believe these two groups, which will spawn for the first time in May and December, are moving north and westward, growing as they go, possibly out of the range of the whalecatchers.

In the second spawning in December and May, when the squids are 79-91 cm mantle length - say 80-90 cm - they are noticed at Talcahuano between April and June, so that there is spawning in May. At Iquique they occur in all months from March onwards, so that there is spawning in May and December. At Pisco and at Paita they are well represented in all months, so again there is spawning off Pisco and Paita in May and December. Further than this we cannot go with Fig. 11.

We accept then Nesis' suggestion that there is a migration of squids from waters off the northern Perú southwards and eastwards towards the coast in summer. Thereafter, we find that the squids are spawning, mostly in May and December, at least from 37°S and probably from 43°S, moving northward with the Current and spreading westward, growing as they go, with a first spawning season off Talcahuano as far as the latitude of Iquique, followed by a second season off Pisco and Paita. The spawning grounds are more extensive than Nesis claimed. But some part of his proposal had to be conjectural because he was sailing in the Southeast Pacific only in late winter and spring, between August and November 1968. Fig. 11 is not the end of the story because there are *D. gigas* off Chile as large as those off Pisco and Paita and we believe that these squids are more abundant off Chile than off Perú.

Further information on the migrations of *D. gigas* is urgently required both for the orderly development of the fishery and for the conservation of the resource. There are occasions when this squid disappears from regions where it may normally be found. Thus in 1997 the owners of foreign squid-fishing vessels paid in advance to the Peruvian government 23 million dollars for permission to take 100 thousand tons of *D. gigas* from the Peruvian sea during eight months of fishing. At the end of this period the foreign vessels had only caught 3,000 tons, and the fishing owners naturally complained (El Comercio, Lima, 14 March 1997).

There is clearly a need for a mark/recapture programme on *D. gigas* undertaken in collaboration by the governments of Ecuador, Chile and Perú. The programme should be well publicised and rewards offered for the return of the marks which presumably would be numbered metal tags clipped on the fins.

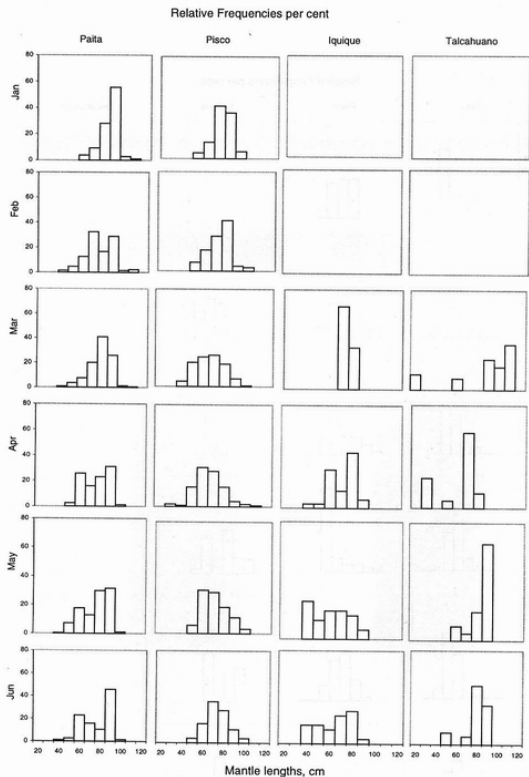


Figure 11

Percentages of mantle lengths at 10 cm intervals of *Dosidicus gigas* measured from sperm whale stomachs in each month of the year at the whaling stations at Paita (05°09'S) in 1959-61, Pisco (13°46'S) in 1960-62, Iquique (20°15'S) in 1960 and Talcahuano (36°40'S) in 1961.

Porcentajes de las longitudes del manto en intervalos de 10 cm de *Dosidicus gigas* medidos de los estómagos de cachalotes en cada mes del año en las estaciones balleneras de Paita (05°09'S) en 1959-61, Pisco (13°46'S) en 1960-62, Iquique (20°15'S) en 1960 y Talcahuano (36°40'S) en 1961.

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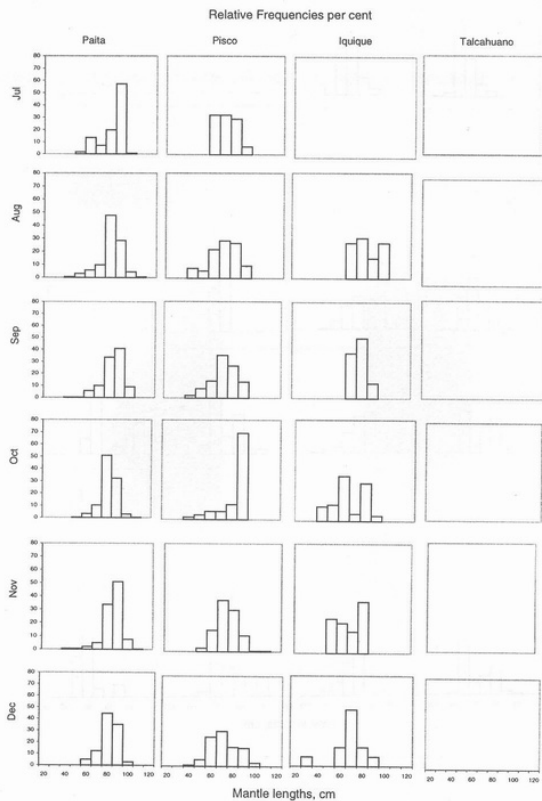


Figura 11 (continued)

Segura *et al.* (1996) have made some preliminary experiments marking 13 of these squids in a tank; 7.7% of the marks came adrift during an average of 13 hours before the squids died, but the authors give no further details.

Presumably it is the sporadic aspect, which sometimes may characterise the migrations of the species, which may have prompted the Peruvian Ministry of Fisheries to designate *D. gigas* a 'Resource of Opportunity'. As the first author said in 1996, six years of a successful fishery do not suggest a 'resource of opportunity' (R Clarke 1996). The designation is unfortunate because it implies (although doubtless not intentionally) that this squid may be exploited whenever opportunity occurs without thought for its conservation.

General exploitation

The data available to us from the squid fishery off Perú refers only to 1989-1992, so we can say very little about the fortunes of exploitation of *D. gigas* from 1992 to the present. We note however that, according to Pesca, Lima, 10 August 1995, the Peruvian government between 1991 and 1994 authorised quotas for this squid, and received tributes for fishing concessions, as shown in Table 9.

Table 9

Fishing for *D. gigas* in Perú: quotas authorised and tributes received by the government.

La pesca de *D. gigas* en el Perú: cuotas autorizadas y tributos recibidos por el gobierno.

	Quota authorised tons	Peruvian government received dollars
1991	90,000	8 million
1992	170,000	26 million
1993	150,000	24 million
1994	170,000	35 million
second quota	70,000	16.45 million

So far as we are aware, these quotas were arbitrarily chosen, being based on no biological assessment. But in 1995 Yamashiro *et al.* (footnote 5), applying Schaefer's model for the period 1991-1995, obtained a maximum sustainable yield for *D. gigas* of 130,895 tons per year with an optimum effort of 164,087 fishing hours. On this basis they recommended a quota in Peruvian waters for 1996 of 100,000 tons which could be adjusted 'according to the behaviour of the resource'.

We have no information on the fortunes of the fishery in 1997-98 when the intensified and disastrous 'El Niño' phenomenon brought warm water of the Equatorial Counter Current against most of the coast of Perú. Possibly the *D. gigas* moved far south off Chile so as to remain in cool water. However, by the end of June 1998 *D. gigas* had again been identified in

Peruvian waters and the Ministry of Fisheries resumed its invitation to foreign vessels to fish this 'sub-exploited resource' ('El Comercio', Lima, 28 June 1998).

Dr Jaime Mendo of the Universidad Nacional Agraria La Molina, Lima, tells us that, using appropriate computer programmes, it should now be possible to obtain figures for natural mortality from the 6,824 specimens of *D. gigas* collected from the stomachs of sperm whales in Chile and Perú between 1959 and 1962. Similar operations carried out on data from the fishery each year will give the instantaneous mortality, and so by subtraction a series of values for the fishing mortality can be obtained. Presumably the natural mortality of these large squids, which have survived until predation by the sperm whale, will be different from that of squids subjected to most other predators and to the fishery, but the exercise would be well worth trying.

The squid and the sperm whale

We have earlier published our concern that the present great fishery for *D. gigas* may put at risk the recovery of the sperm whale stock in the Southeast Pacific (R Clarke *et al.* 1992, footnote 3, 1993, R Clarke & Paliza 1995, R Clarke 1996), but we consider that the matter should again be emphasised in an international journal, especially since in 1999 the International Whaling Commission is expected to examine the present condition of the world sperm whale stocks.

R Clarke *et al.* (1988, p. 90, 94) found that flesh remains of *D. gigas* were present in 99.91% of 1,123 male sperm whales and 99.49% of 784 females whose stomachs contained food in Chile and Perú between 1959 and 1962: one or other of two more species of squid were present in the stomachs of 0.09% of these males and 0.51% of the females; fish were only present in 0.62% of males and 0.13% of females. So *D. gigas* is virtually the only food of sperm whales in the Southeast Pacific.

We have already noted that, according to R Clarke *et al.*'s estimate (1988, p. 115-141, Tables 24-41), the stock of sperm whales in the Southeast Pacific between 1959 and 1961 was consuming each year, between appropriate confidence limits, 8.69 million tons of *D. gigas* based on the normal complete meal and 13.67 million tons based on the complete meal to satiety. During these years also sperm whales in the Southeast Pacific had reached their maximum sustainable yield and by 1963 were being over-exploited (Saetersdahl *et al.* 1963). In 1982 the International Whaling Commission prohibited sperm whaling in the Southeast Pacific.

Now we are in no way suggesting that fishing quotas

for *D. gigas* like 240,000 tons in Perú in 1994, or similar ones, whatever they may be, in Chile and Ecuador, may together or by themselves affect the recovery of the sperm whale stock in this area. But other factors intervene. First there is the tendency for quotas to increase progressively in the Southeast Pacific. We recall the enormous quotas of anchoveta for the fish meal industry which led to the collapse of the anchoveta stock off Perú in the nineteenth century, with the consequent mass mortalities of guano birds and reduction in the guano harvest. Nor should we forget the gross over-exploitation of the sperm whale stock off Chile and Perú. Secondly the fishery is taking much smaller animals from the *D. gigas* stock than do the sperm whales. The squids caught by the jigging machines weigh only a few kilograms each, whereas, as we have earlier noticed, the average weight of a squid swallowed by a large male sperm whale, between 12 and 18 m long, is 25.7 kg, and female sperm whales and small males (6.0-11.9 m long) eat specimens which each weigh on average 17.5 and 17.2 kg respectively (R Clarke *et al.* 1988, p. 99, Table 14). Now between 1989 and 1992 there were 25.6% sexually immature squids among 43,256 *D. gigas* fished off Perú, whereas only ten *D. gigas*, or 0.21%, were sexually immature among the 4,872 specimens recovered from sperm whale stomachs between 1959 and 1962 in Chile and Perú. The squids eaten by sperm whales had almost all spawned at least once and many of them twice. *D. gigas* is a key organism in the ecosystem of the Humboldt Current and the modern fishery is competing with all those predators of *D. gigas* we have listed above and these probably take squids of similar size to those taken by the fishery, so that the proportions sexually immature are likely to increase. The sperm whale takes larger squids and is not competing with the fishery or with the other predators. But we are concerned that, without adequate control, the number of recruits to the food reservoir of the sperm whale may eventually be diminished to an extent which threatens the recovery of the sperm whale stock in the Southeast Pacific.

Recommendation

D. gigas and the reduced stock of sperm whales in the Southeast Pacific are in a parallel situation to the krill (*Euphausia superba*) and the reduced stocks of whalebone whales in the Antarctic. All these species of whalebone whales, at present protected, like the sperm whales, by the International Whaling Commission, feed exclusively on krill when they are in the Antarctic in summer, whilst over the years there has developed a considerable Antarctic fishery for krill for human consumption by vessels of various nationalities. But in the Antarctic this situation has been monitored since 1979 by an International Convention on Living Marine

Resources of the Antarctic. The Convention set up a Committee which has since met 15 times. Something similar is required in the Southeast Pacific.

So far as we are aware there is only a single stock of *D. gigas* in the Humboldt Current and its extension as the South Equatorial Current to the Galápagos Islands. We therefore recommend that Chile, Ecuador and Perú join forces in a single programme of research which we suggest should be coordinated by the Permanent Commission of the South Pacific. This programme should lead to a stock assessment of *D. gigas* which in turn would provide appropriate fishing quotas. The assessment would require cruises, fishing and making sonar counts, across the Current at regular intervals, quite independent of commercial fishing; and there should also be mark/recapture programmes to investigate, not only migration, but also one approach to abundance.

Osako & Murata (1983) attempted a stock assessment of two squid species in the North Pacific, and since then there have been assessments by a variety of methods for five other species (Boyle & Bolensky 1996, Table 3). Surprisingly, MR Clarke (1996 b, Table 1) has published an estimate of the stock of *D. gigas* in the Southeast Pacific as 1.3 million – 18 million tons, with no indication how this was achieved; from what we know of the predation of the sperm whale alone on *D. gigas* this must be an underestimate, and the field for stock assessment of the Humboldt Current squid is still open and urgent.

The project would not be an easy one. Specialists in stock assessment and in modelling would be required. But the money is surely available as a fraction of the hundreds of millions of dollars which the governments now receive for permission to fish *D. gigas* in their territorial seas. Meanwhile we suggest as a preliminary measure that consideration should be given to making the months of May and December closed seasons to protect the spawning squids.

By such a cooperative programme we believe that this great fishery for the Humboldt Current squid can be assured into the future, and we also hope that the sperm whale stock, adequately sustained by *D. gigas*, will have sufficiently recovered, in the not too distant future, to be exploited again, but this time under strict control, in the Southeast Pacific.

Summary

The present great fishery for *D. gigas* in the Southeast Pacific, using automatic jigging machines, arose in 1989 from a recommendation by R Clarke *et al.* (1988, p. 141). In each section, after reviewing previous work, the present report examines data from the fishery and

data from squids removed from sperm whale stomachs to try and increase our knowledge of the biology, life history and migrations of *D. gigas* and to make a recommendation for the future management of the fishery.

Our material comprises data from 6,824 unsexed specimens of *D. gigas* from sperm whale stomachs examined in Chile and Perú between 1959 and 1962 and 43,256 sexed specimens from Japanese and Korean vessels fishing off the coast of Perú between 1989 and 1992.

We put the maximum dimensions of *D. gigas* at 1.2 m mantle length, 2.2 m standard length and 2.6 m total length, with maximum weight 65 kg. Regressions by various authors of total or partial body weight on mantle length for *D. gigas* from the fishery are compared with those for this squid from sperm whale stomachs. After reviewing the horizontal distribution of *D. gigas* we conclude that the populations in the northern and southern hemispheres are distinct, possibly sub-species. The southern population is restricted to the cool water of the Humboldt Current from far south of Chile including its extension as the South Equatorial Current to the Galápagos Islands. The distribution of this population further north is restricted by the warm Equatorial Counter Current. The northern population lives in warm water and the squids are smaller than those in the south. We distinguish the two populations as the Humboldt Current squid and the Gulf of California squid, whilst both retain the same specific name *Dosidicus gigas* until such time as morphometric data from the southern population may be compared with Wormuth's Table 8 (1976) showing the morphometry of the northern population. Analysis of DNA might also be compared between the two populations. We consider that the vertical distribution of *D. gigas* is from the surface to about 300 m and that the species shows ontogenetic descent. Colour changes at death are noticed and bioluminescence is discussed. Changes in the diet of *D. gigas* during ontogeny are examined: it has been possible to identify the species of squid eaten by large *D. gigas*. We discuss cannibalism and note that the unequal and changing sex ratio from an early age can only be explained by predation of females on males. The predators of *D. gigas* are reviewed. The sperm whale takes large *D. gigas* each of average weight between 17.2 and 25.7 kg according to the sex and size of the whales. R Clarke *et al.* (1988, p. 90-94, p. 99) have explained why MR Clarke's statement (1982-1985), that the average weight of all squid eaten by sperm whales off Western South America is 1.3 kg, is unacceptable. The sperm whale is not competing with other predators nor with the fishery. Two recent papers deal with parasites in *D. gigas* fished off Perú. Most squids are parasitized by larvae of the nematode

Anisakis sp. and also by plerocercoid larvae of the cestode *Tentacularia* sp. We show that the nematode is *Anisakis physeteris* which, with the much less common *A. simplex*, are the only species of *Anisakis* identified from sperm whale stomachs in the Southeast Pacific. Then in this ocean *D. gigas* is a primary host of *A. physeteris*, and probably of *A. simplex*, and the sperm whale is a secondary host. 'Human anisakiasis', due to eating raw squids and fish, is mentioned.

Tafur & Rabi (1997) give the best estimates for the mantle length of *D. gigas* at sexual maturity: 29 cm in males and 32 cm in females. Using data from the fishery (1989-92) we examine the changing sex ratios to show that there are two abrupt increases in the proportion of females, at 31-40 cm mantle lengths and at 91-100 cm, and these female peaks are in May and December. We propose that these are the mantle lengths at the first and the second spawning seasons respectively, either May or December, the months of intense copulation and of post-copulatory cannibalism of the males by the females. From 777 squids measured and weighed (but not sexed) at Pisco in 1962, we compare lengths and weights of the mantles using a Condition Index calculated and afterwards plotted for each month of the year. The curve shows two strong peaks in April and November when the squids are heaviest. These are the months when females are heavy with ripe eggs and the males are ready with their spermatophores. Spawning takes place in the following months, May and December, as indicated by the sex ratios.

We use data from Masuda *et al.*'s work on statoliths (1998) to propose constant growth rates of 6.6 cm and 7.6 cm per month respectively for males and females. There may be some changes in these rates during ontogeny, but on this our data provide no information. We argue that squids spawned in December spawn for the first time after five months in May; those spawned in May are late spawning in December. There is a second spawning in December and May respectively, when all the squids are 12 months old. At constant growth rates the maximum life span or longevity is 15 months for males and 16 months for females.

We show that growth is not isometric in *D. gigas*; the head-and-arms grow faster than the mantle, an adaptation to the catching of larger prey as the squid grows.

There is reason to believe that *D. gigas* is more abundant off Chile than off Perú. Like Nesis (1970) we believe that squids spawned off the length of the coast of Perú in winter and spring are to be found off Chile in summer. Using histograms showing the sizes of *D. gigas* each month from sperm whale stomachs at Paita (05°09'S), Pisco (13°46'S), Iquique (20°15'S) and

Talcahuano (36°40'S), we find that squids are spawning, mostly in May and December, from 37°S, and probably from 43°S, moving northward with the Current and spreading westward, growing as they go, with a first spawning season off Talcahuano and Iquique, followed by a second season off Pisco and Paita. We urgently need to know more about migrations of *D. gigas*. Meanwhile there is no reason to believe that there is more than one stock of this squid in the Humboldt Current.

Whereas in 1959-62 only 0.21% of *D. gigas* from sperm whale stomachs in Chile and Perú were sexually immature, there were 25.6% immature among those fished off Perú in 1989-92. We are concerned that this proportion may increase to threaten not only the fishery but the recovery of the sperm whale stock in the Southeast Pacific. We therefore recommend that Chile, Ecuador and Perú should join forces in a single programme of research on *D. gigas* which we suggest should be coordinated by the Permanent Commission of the South Pacific. This programme should lead to a stock assessment which would provide appropriate fishing quotas. The programme would include cruises, fishing and making sonar counts across the Current independent of commercial fishing, and there should also be mark/recapture programmes. The undertaking can be financed by a fraction of the hundreds of millions of dollars which the governments receive for permission to fish *D. gigas* in their territorial seas.

Meanwhile it is proposed that May and December be made closed seasons to protect the spawning squids.

Sumario

La gran pesca actual de *D. gigas* en el Pacífico Sureste, usando máquinas de aparejo automático, surgió en 1989 de una recomendación por R Clarke *et al.* (1988, p. 141). Después de revisar trabajos anteriores el presente informe examina datos de la pesca y datos de calamares sacados de los estómagos de cachalotes para tratar de aumentar nuestro conocimiento sobre la biología, historia de la vida y migraciones de *D. gigas* y hacer una recomendación para el futuro manejo de la pesca.

Nuestro material comprende datos de 6.824 especímenes, cuyos sexos no fueron determinados, de *D. gigas* de los estómagos de cachalotes examinados en Chile y Perú entre 1959 y 1962; y de 43.256 especímenes donde los sexos fueron determinados, pescados frente a la costa del Perú por embarcaciones japonesas y coreanas entre 1989 y 1992.

Nosotros ponemos las dimensiones máximas de *D. gigas* a 1,2 m de longitud de manto, 2,2 m de longitud estándar y 2,6 m de longitud total, con peso máximo de 65 kg. Regresiones dadas por varios autores del peso

total o parcial del cuerpo sobre la longitud del manto para *D. gigas* de la pesca, son comparadas con aquellas para este calamar de los estómagos de cachalotes. Después de revisar la distribución horizontal de *D. gigas* concluimos que las poblaciones en los hemisferios norte y sur son distintas, posiblemente sub-especies. La población del sur está restringida al agua fría de la Corriente de Humboldt desde el sur de Chile incluyendo su extensión como la Corriente Sud-Ecuatorial hasta las Islas Galápagos. La distribución de esta población más al norte está restringida por la cálida Contra Corriente Ecuatorial. La población del norte vive en aguas cálidas y los calamares son más pequeños que aquellos en el sur. Nosotros distinguimos las dos poblaciones como el calamar de la Corriente de Humboldt y el calamar del Golfo de California, mientras que ambos retienen el mismo nombre específico *Dosidicus gigas* hasta que se pueda comparar datos morfométricos de la población del sur con la Tabla 8 de Wormuth (1976) que muestra la morfometría de la población del norte. También se podría comparar el análisis del ADN entre las dos poblaciones. Consideramos que la distribución vertical de *D. gigas* es desde la superficie hasta alrededor de 300 m y que la especie muestra descenso ontogenético. Se notan los cambios de color al morir y se discute bioluminiscencia. Los cambios en la dieta de *D. gigas* durante la ontogenia son examinados: ha sido posible identificar las especies de calamares comidos por grandes *D. gigas*. Discutimos el canibalismo y notamos que la relación de los sexos, desigual y cambiante desde una edad temprana, solamente se puede explicar por la predación de hembras sobre machos. Se revisan los predadores de *D. gigas*. El cachalote captura grandes *D. gigas* cada uno con un peso promedio entre 17,2 y 25,7 kg de acuerdo al tamaño y sexo de las ballenas. R Clarke *et al.* (1988, p. 90-94, p. 99) han explicado por qué es inaceptable la declaración de MR Clarke (1982-1983), de que el peso promedio de todos los calamares comidos por el cachalote frente a la costa oeste de América del Sur es 1,3 kg. El cachalote no está compitiendo con otros predadores ni con la pesca. Dos trabajos recientes tratan sobre parásitos de *D. gigas* pescados frente a Perú. La mayoría de los calamares son parasitados por larvas del nemátodo *Anisakis* sp. y también por la larva plerocercario del cestodo *Tentacularia* sp. Nosotros mostramos que el nemátodo es *Anisakis physeteris* el cual, con el mucho menos común *A. simplex*, son las únicas especies de *Anisakis* identificadas de los estómagos de cachalotes en el Pacífico Sureste. Entonces en este océano *D. gigas* es un huésped primario de *A. physeteris* y probablemente de *A. simplex*, y el cachalote es un huésped secundario. Se menciona la enfermedad 'anisaquiasis humana', por comer calamares y pescado crudos.

Tafur & Rabi (1997) dan las mejores estimaciones

para la longitud del manto de *D. gigas* a la madurez sexual: 29 cm en machos y 32 cm en hembras. Usando los datos de la pesca (1989-92) examinamos los cambios en la relación de sexos para mostrar que hay dos aumentos abruptos en la proporción de hembras, a 31-40 cm de longitud del manto y a 91-100 cm, y estos picos para hembras están en mayo y diciembre. Nosotros proponemos que éstas son las longitudes de manto a la primera estación de desove y a la segunda, sea en mayo o en diciembre, los meses de intensa copulación y de canibalismo post-copulatorio de los machos por las hembras. Nuestro acercamiento al ciclo sexual y la longevidad en *D. gigas* es principalmente a través de los 777 calamares medidos y pesados (pero cuyos sexos no fueron determinados) en Pisco en 1962. Comparamos la longitud del manto y el peso del manto usando un Índice de Condición, calculado y luego graficado para cada mes del año. La curva muestra dos fuertes picos en abril y en noviembre cuando los calamares están más pesados. Estos son los meses cuando las hembras maduras están pesadas por los huevos maduros y los machos están listos con sus espermatozoides. El desove toma lugar en los meses siguientes, mayo y diciembre, como es indicado por los cambios en la relación de sexos. Nosotros usamos los datos del trabajo de Masuda *et al.* (1998) sobre los estatolitos para proponer tasas de crecimiento constantes de 6,6 cm y 7,6 cm por mes para machos y hembras respectivamente. Puede que haya algunos cambios en estas tasas durante la ontogenia, pero sobre esto nuestros datos no dan información. Argumentamos que los calamares desovados en diciembre desovan por primera vez después de cinco meses en mayo; aquellos desovados en mayo son los que desovan tardíamente en diciembre. Hay un segundo desove en diciembre y mayo respectivamente, cuando todos los calamares tienen 12 meses de edad. A tasas de crecimiento constantes la amplitud máxima de vida o longevidad es de 15 meses para los machos y de 16 meses para las hembras.

Nosotros mostramos que el crecimiento en *D. gigas* no es isométrico, la cabeza-y-los-brazos crecen más rápido que el manto, una adaptación a la captura de presas más grandes conforme el calamar crece.

Hay razón para creer que *D. gigas* es más abundante frente a Chile que frente a Perú. Como Nesis (1970), nosotros creemos que los calamares desovados frente a lo largo de la costa de Perú en invierno y primavera van a ser encontrados frente a Chile en verano. Usando histogramas que muestran los tamaños mensuales de *D. gigas* de los estómagos de cachalotes en Paita (05°09'S), Pisco (13°46'S), Iquique (20°15'S) y Talcahuano (36°40'S), encontramos que los calamares están desovando en mayo y diciembre, desde 37°S, y probablemente desde 43°S, moviéndose hacia el norte con la corriente y desparramándose hacia el oeste,

creciendo conforme avanzan, con la primera estación de desove frente a Talcahuano e Iquique, seguido por una segunda estación frente a Pisco y Paita. Necesitamos urgentemente saber más sobre las migraciones de *D. gigas*. Mientras tanto no hay razón para creer que haya más de una existencia de este calamar en la Corriente de Humboldt.

Mientras que en 1959-62 solamente un 0,21% de *D. gigas* de los estómagos de cachalotes en Chile y Perú eran sexualmente inmaduros, hubo un 25,6% de inmaduros entre aquellos capturados frente a Perú en 1989-92. Nos preocupa que esta proporción pueda aumentar hasta amenazar no solamente la pesca sino también la recuperación de la existencia del cachalote en el Pacífico Sureste. Por lo tanto nosotros recomendamos que Chile, Ecuador y Perú deberían juntarse en un solo programa de investigación de *D. gigas* el cual sugerimos debería ser coordinado por la Comisión Permanente del Pacífico Sur. Este programa conduciría a una tasación de la población la cual proporcionaría cuotas de pesca adecuadas. El programa incluiría cruceros, de pesca y de conteos con sonar, a través de la Corriente independientes de la pesca comercial, y debería también haber programas de marcación/recaptura. La investigación puede ser financiada con una fracción de los cientos de millones de dólares que los gobiernos reciben por concesiones para pescar *D. gigas* en sus mares territoriales.

Mientras tanto se propone que mayo y diciembre sean estaciones de veda para proteger a los calamares desovantes.

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The data on *Dosidicus gigas* from sperm whale stomachs derive from the whaling investigations conducted in Chile, Ecuador and Perú between 1958 and 1962 with the help of the Food and Agriculture Organization of the United Nations and under the auspices of the Permanent Commission of the South Pacific. R Clarke *et al.* (1968, Part I) have explained how these investigations arose and they have thanked all those who helped to advance the investigations, including the names of those biologists who collaborated in the examination of sperm whale carcasses, which included the most unpleasant task of examining the stomach contents and which they carried out with dedication.

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Literature Cited

- Argüelles TJ. 1996. Crecimiento y reclutamiento del calamar gigante *Dosidicus gigas* en el Perú (1991 a 1994). Informe Progresivo del Instituto del Mar del Perú, Callao. 23, 14 p.
- Arkhipkin AI & SA Murzov. 1986. Statolith morphology, growth and development in Squids of the family Ommastrephidae from South-eastern part of the Pacific. *Oceanic Zoology Zh.* 64: 499-505.
- Baylis HA. 1923. An ascidian from a sperm whale. *Annals of the Magazine of Natural History*, London 9: 211-217.
- Beale T. 1839. *The Natural History of the Sperm Whale*. to which is added a Sketch of A South-Sea Whaling Voyage. London, John van Voorst, 393 p.
- Benham WB. 1901. The Platyhelminia, Mesozoa and Nemertini. In: E. Ray Lankester (ed), *A Treatise on Zoology*, Part IV, 204 p. Adam and Charles Black, London.
- Benites C & V Valdivieso. 1986. Resultados de la pesca exploratoria de 1979/80 y desembarque de cefalópodos pelágicos en el litoral peruano. *Boletín del Instituto del Mar del Perú*, Callao 10: 108-139.
- Berzin AA. 1971. *Kashalot. Izdatel'stvo "Pishevaya Promyshlennost"*, Moskva. Consulted in English translation, The sperm whale. Israel Program for Scientific Translations, Jerusalem, 1972, 394 p.
- Blunt CE. 1968. Observations on the food habits of longline caught bigeye and yellowfin tuna from the tropical eastern Pacific 1955-56. *California Fish and Game* 46: 69-80
- Boone L. 1933. Scientific results of cruises of the yachts 'Eagle' and 'Ara', 1921-1928. *Mollusca. Bulletin of the Vanderbilt Marine Museum* 4: 165-210.
- Borradaile LA, LES Eastham, FA Potts & JT Saunders. 1935. *The invertebrata*. Cambridge University Press, 725 p.
- Boyle FR & SV Boletzky. 1996. Cephalopod populations: definition and dynamics. P. 985-1002. In: MR Clarke (ed), *The role of cephalopods in the world's oceans*. *Philosophical Transactions of the Royal Society of London. Series B* 351: 977-1112.
- Buen F de. 1959. Notas sobre ictiología chilena con descripción de dos especies nuevas. *Revista de Biología Marina* 9: 257-270.
- Caddy JF (ed.). 1983. *Advances in Assessment of World Cephalopod Resources*. FAO Fisheries Technical Paper 231, 452 p.
- Clark FN & JB Phillips. 1936. Commercial use of the jumbo squid *Dosidicus gigas*. *California Fish and Game* 22: 143-144.
- Clarke MR. 1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. *Bulletin of the British Museum (Natural History). Zoology* 8: 419-480.
- Clarke MR. 1965. Large light organs on the dorsal surfaces of the squids *Ommastrephes pteropus*, '*Symplectoteuthis oualaniensis*' and '*Dosidicus gigas*'. *Proceedings of the Malacological Society, London* 36: 319-321.
- Clarke MR. 1966. A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology* 4: 93-327.
- Clarke MR. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37: 1-324.
- Clarke MR. 1982-83. *Cephalopoda*. McGraw-Hill Yearbook of Science & Technology: 153-156.
- Clarke MR. (ed.). 1996. *The role of cephalopods in the world's oceans*. *Philosophical Transactions of the Royal Society of London. Series B* 351: 977-1112.
- Clarke MR. 1996a. Cephalopods as prey. III. Cetaceans. 1105-1112. In: MR Clarke (ed). *The role of cephalopods in the world's oceans*. *Philosophical Transactions of the Royal Society of London. Series B* 351: 977-1112.
- Clarke MR. 1996b. The role of cephalopods in the world's oceans: general conclusions and the future. P. 1105-1112. In: MR Clarke (ed.). *The role of cephalopods in the world's oceans*. *Philosophical Transactions of the Royal Society of London. Series B* 351: 977-1112.
- Clarke MR, N MacLeod & O Paliza. 1976. Cephalopod remains from the stomachs of sperm whales caught off Peru and Chile. *Journal of Zoology*, London 180: 477-493.
- R. Clarke. 1955. A giant squid swallowed by a sperm whale. *Norsk Hvalfangst-Tidende* 10: 589-593.
- Clarke R. 1962. Whale observation and whale marking off the coast of Chile in 1958 and from Ecuador towards and beyond the Galápagos Islands in 1959. *Norsk Hvalfangst-Tidende* 51: 265-287.
- Clarke R. 1996. Investigación para explotar racionalmente la pota. *El Comercio*, Lima. Carta del lector, 15 de julio de 1996.
- Clarke R, A Aguayo L & S Basulto del Campo. 1978. Whale observation and whale marking off the coast of Chile in 1964. *Scientific Reports of the Whales Research Institute, Tokyo* 30: 117-177.

- Clarke R, A Aguayo L & O Paliza. 1968. Sperm whales of the Southeast Pacific. Part I. Introduction. Part II. Size range, external characters and teeth. *Hvalrådets Skrifter* 51, 80 p.
- Clarke R & O Paliza. 1995. A Contracorriente. Caretas, Lima, 1366: 26-27.
- Clarke R, O Paliza & A Aguayo L. 1980. Some parameters and an estimate of the exploited stock of sperm whales in the Southeast Pacific between 1959 and 1961. Report of the International Whaling Commission 30: 289-305.
- Clarke R, O Paliza & A Aguayo L. 1988. Sperm whales of the Southeast Pacific. Part IV: Fatness, food and feeding. Investigations on Cetacea (ed. G. Pilleri) 21: 53-195.
- Clarke R, O Paliza & A Aguayo L. 1993. Riesgo para la recuperación de la existencia de cachalotes en el Pacífico Sureste debido al desarrollo de la pesca de la pota. *Boletín de Lima*, 85: 73-78.
- Colnett, Captain J. 1798. A Voyage to the South Atlantic and round Cape Horn into the Pacific Ocean for the purpose of extending the Spermaceti Whale Fisheries.....London, 179 p.
- Croxall JF & PA Prince. 1996. Cephalopods as prey. I. Seabirds. P. 1023-1043. In: MR: Clarke (ed.), The role of cephalopods in the world's oceans. Philosophical Transactions of the Royal Society of London. Series B 351: 977-1112.
- Deadorff T & RM Overstreet. 1991. Seafood-transmitted zoonoses in the United States: the fishes, the dishes and the worms. P. 211-265. In: D Ward & C Hackney (eds), Microbiology of Marine Food Products: Na AVI Book, New York.
- Delyamure SL & AS Skryabin. 1971. Helminths. P. 274-300. In: AA Berzin. *Kashalot. Izdatel'stvo "Pishchevaya Promyshlennost"*, Moskva. Consulted in English translation, The sperm whale. Israel Program for Scientific Translations, Jerusalem, 1972: 394 p.
- Duncan DD. 1941. Fighting Giants of the Humboldt. National Geographic Magazine. 79: 373-400.
- El Comercio, Lima. 1997. Extractores extranjeros de pota se retirarán del mar peruano. 14 de marzo de 1997.
- El Comercio, Lima. 1998. Facilitan pesca de la pota. 28 de junio de 1998.
- Erhardt NM, PS Jacquemin, F García, G González, JM López, J Ortiz & A Solis. 1983. On the Fishery and Biology of the Giant Squid *Dosidicus gigas* in the Gulf of California, Mexico. P. 264-305. In: JF Caddy (ed). Advances in Assessments of World Cephalopod Resources FAO Fisheries Technical Paper 231: 452 p.
- Fernández F & JA Vásquez. 1995. La jibia gigante *Dosidicus gigas* (Orbigny, 1835) en Chile: análisis de una pesquería efímera. *Estudios Oceanológicos* 14: 17-21.
- Fusejima I. 1993. Report of the Survey on Jumbo Flying Squid in the Ecuadorian and adjacent Waters, organised jointly by Instituto Nacional de Pesca (INP) and Japan Marine Fishery Resources Center (JAMARC) carried out by Shinko Maru No. 2 from 12 November to 29 December 1992. JAMARC. Report No. 20/ 1992 21 p. Tokyo, Japan.
- García-Tello P. 1964. Nota preliminar sobre una observación de bioluminiscencia en *Dosidicus gigas* (d'Orb.) Cephalopoda. *Boletín de la Universidad de Chile*, 46: 27-28.
- García-Tello P. 1965. Utilización de la mandíbula inferior de la jibia *Dosidicus gigas* (d'Orb.) en el cálculo de su peso total (Mollusca, Cephalopoda, Ommastrephidae). *Revista de Biología Marina, Valparaíso* 12: 185-197.
- González J & J Mendo. (in press) Larvas helmintos en el "calamar gigante" *Dosidicus gigas* (Ommastrephidae) de la costa norte del Perú. *Anales Científicos de la Universidad Nacional Agraria La Molina, Lima, Perú*.
- Gunther ER. 1936. A report on oceanographical investigations in the Peru Coastal Current. *Discovery Reports* 13: 107-276.
- Huxley JS. 1932. Problems of relative growth. London.
- Icaza R. 1979. Informe sobre el convenio de cooperación técnica entre el gobierno del Ecuador y La Compañía K. & L. Limited en Tokyo, Japón, sobre investigación para establecer la factibilidad de la pesca de calamares en aguas ecuatorianas. Informes Pesqueros del Instituto Nacional de Pesca, Ecuador, 13: 92 p.
- Instituto del Mar del Perú and Japan Marine Resources Research Centre. 1991. Joint survey report on jumbo flying squid conducted by Instituto del Mar del Perú (IMARPE) and Japan Resources Research Centre (JAMARC) by Shinko Maru No. 2 (In the waters Peruvian 200-mile zone, including adjacent waters). From 4 November to 17 December 1989. JAMARC Report 18, 58 p.
- International Whaling Commission. 1982. Chairman's Report of the Thirty-third Meeting. Report of the International Whaling Commission 32: 17-42.
- Kuroiwa M. 1998. Exploration of the Jumbo Squid, *Dosidicus gigas*, Resources in the Southeastern Pacific Ocean with Notes on the History of Jigging Surveys by the Japan Marine Fishery Resources Research Center. P. 85-105. In: T Okutani (ed). Contributed papers to international symposium on large pelagic squids, July 18-19, 1996: Japan Marine Fishery Research Centre (JAMARC), Tokyo, June 1998.
- Lane FW. 1957. Kingdom of the Octopus. The Life-History of the Cephalopoda. Jarrolds, London, 287 p.
- Lee H. 1875. The octopus; or, the 'devil-fish' of fiction and fact. London, Chapman & Hall. 114 p.
- Mariátegui L & A Taipe. 1996. Distribución y abundancia relativa del calamar gigante (*Dosidicus gigas*) en el Perú. Informe Progresivo del Instituto del Mar del Perú-Callao, 34: 27 p.

- Masuda S, K Yokawa, S Kawahara & A Yatsu. 1996.** Age determination in the middle sized giant squid *Dosidicus gigas* off Perú. In: Report of 1994 Annual Meeting on Resources and Fisheries on Squids, Hokkaido Natural Resources and Fisheries Institute: P. 123-132 (in Japanese).
- Masuda S, K Yokawa, A Yatsu & S Kawahara. 1998.** Growth and Population Structure of *Dosidicus gigas* in the Southeastern Pacific Ocean. P. 107-118 In: T Okutani (ed), Contributed papers to international symposium on large pelagic squids, July 18-19, 1996: Japan Marine Fishery Research Centre (JAMARC), Tokyo, June 1998.
- Molina GL 1782.** Saggio sulla storia naturale del Chile Libro IV, Bologna. 367 p.
- Molina GL 1788.** Compendio Historia y Geografía Natural y Civil del Reino de Chile. Madrid.
- Nesis KN. 1970.** The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. Oceanology (English translation) 10: 108-118.
- Nesis KN. 1983.** *Dosidicus gigas*. P. 215-231. In: P.R. Boyle (ed.), Cephalopod Life Cycles. Vol. I: Species Accounts. Academic Press, London.
- Nigmatullin ChM, P Fedoulov & AZ Sundakov. 1995.** Review of USSR/Russia Cephalopod Fishery in 1980-1994. Proceedings of Squid 94, Venice, Agra Europe. 11 p.
- Okutani T (ed.). 1998.** Contributed papers to international symposium on large pelagic squids, July 18-19, 1996. Japan Marine Fishery Research Centre (JAMARC), Tokyo, June 1998.
- Orbigny A d'. 1835-43.** Voyage dans l'Amérique meridionale. Paris, Vol. 5, Partie 3, Mollusques, 758 p.
- Orr RT. 1966.** Risso's dolphin on the Pacific coast of North America. Journal of Mammalogy 47: 341-343.
- Osako M. & M Murata. 1983.** Stock assessment of cephalopod resources in the Northwestern Pacific. P. 55-144. In: JF Caddy (ed.), Advances in Assessment of World Cephalopod Resources. FAO Fisheries Technical Paper 231: 452 p.
- Pelenseer P. 1906.** Mollusca. Part V, 355 p. In: ER Lankester (ed.) A. Treatise on Zoology, Adam and Charles Black, London.
- Perrin WF, RR Warner, CH Fiscus & DB Holts. 1973.** Stomach contents of Porpoise, *Stenella spp.*, and Yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fishery Bulletin 71: 1077-1092.
- Pesca, informe de Caretas, Lima, 10 de agosto, 1995.** P. 8-9, Potente Pota.
- Pitman RL & LT Ballance. 1992.** Parkinson's petrel. Distribution and foraging ecology in the Eastern Pacific: aspects of an exclusive relationship with dolphins. Condor 94: 825-835.
- Rodhouse PG & ChM Nigmatullin. 1996.** Role as consumers. P. 1003-1022. In: MR Clarke (ed). The role of cephalopods in the world's oceans. Philosophical Transactions of the Royal Society of London. Series B 351: 977-1112.
- Roper CFE. 1963.** Observations on bioluminescence in *Ommastrephes pteropus* (Steenstrup, 1855), with notes on its occurrence in the family Ommastrephidae (Mollusca, Cephalopoda). Bulletin of Marine Science, Gulf and Caribbean 13: 343-353.
- Roper CFE & RE Young. 1975.** Vertical distribution of pelagic cephalopods. Smithsonian Contributions, Zoology 209: 1-51.
- Roper CFE, MJ Sweeney & CE Nauen. 1984.** FAO species catalogue. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 125, Vol 3, 277 p.
- Rubio J & C Salazar. 1992.** Prospección pesquera del calamar gigante (*Dosidicus gigas*) abordo del buque japonés Shinko Maru 2 (04 de Noviembre - 17 de Diciembre de 1989). Informe del Instituto del Mar del Perú-Callao 103, 31 p.
- Saetersdal G, J Mejía & P Ramírez. 1963.** La caza de cachalotes en el Perú. Estadísticas de captura para los años 1947-1961 y un intento de analizar las condiciones de la población en el período 1954-1961. Boletín del Instituto de Investigación de los Recursos Marinos, Callao 1: 45-84.
- Sato T. 1976.** Results of exploratory fishing for *Dosidicus gigas* (D'Orbigny) off California and Mexico. FAO Fisheries Reports 170, Suppl. 1: 61-67.
- Schott G. 1931.** Der Peru-Strom und seine nordlichen Nachbargebiete in normaler und anormaler Ausbildung. Annalen für hydrographie, Berlin 59: 161-9, 200-13, 240-52.
- Schott G. 1943.** Nachtrag zu dem Aufsatz "Die Grundlagen einer Weltkarte de Meeresströmungen". Annalen für hydrographie, Berlin, 7: 281-282, chart 22.
- Schweigger E. 1947.** El litoral Peruano. Lima, Compañía Administradora del Guano, 262 p.
- Segura M, R Castillo, J Rubio, E Tello, M Gutiérrez & A Aliaga. 1996.** Cruce de investigaciones sobre el recurso calamar gigante o pota a bordo del BICSNP-1CR.9510-11. Informe Progresivo del Instituto del Mar del Perú-Callao 34: 29-65.
- Streenstrup JJS. 1881.** Prof. A. E. Verrills to nye Cephaloposlaegter: *Stenoteuthis* og *Lestoteuthis* Bemærkninger og Berigtigelse. Overset over det kongelige danske Videnskabernes Selskabs. Forhandling: 1-27.
- Sylva DP de. 1962.** Red-Water Blooms off Northern Chile, April-May 1956, with Reference to the Ecology of the Swordfish and the Striped Marlin. Pacific Science 16: 271-279.

- Tafur R & M Rabi. 1997.** Reproduction of the jumbo flying squid *Dosidicus gigas* (Cephalopoda, Ommastrephidae) (Orbigny, 1835) off Peruvian coasts. *Scientia Marina* 61 (Supl. 2): 35-39.
- Torres ND. 1987.** Juan Fernández fur seal, *Arctocephalus philippii*. P. 37-41. In: JP Croxall & RL Gentry (eds). Status, biology and ecology of fur seals. NOAA Technical Report NMFS 51.
- Voss GL & RF Sisson. 1967.** Squids: Jet-powered Torpedoes of the Deep. *National Geographic Magazine* 131: 386-411.
- Voss NA, M Vecchione, RB Toll & MJ Sweeney (eds). 1998.** Systematics and Biogeography of Cephalopods. *Smithsonian Contributions to Zoology* 586. Vol. 1: 1-276; Vol. 2: 277-599, Washington D.C.
- Wilhelm O. 1930.** Las mortandades de jibias (*Ommastrephes gigas*) en la Bahía de Talcahuano. *Boletín de la Sociedad de Biología de Concepción* (Chile) 3 y 4 (1929-30): 23-28.
- Wilhelm O. 1954.** Algunas observaciones acerca de las mortandades de jibias (*Dosidicus gigas* d'Orb.) en el litoral de Concepción. *Revista de Biología Marina* 4: 196-201.
- Wormuth JH. 1976.** The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. *Bulletin of the Scripps Institute of Oceanography* 23; 90 p.
- Wormuth JH. 1998.** Deliberation on the Ommastrephidae: A brief history of their systematics and a review of the systematics, Distribution and biology of the genera *Martialia* Rochebrune and Martilla, 1889, *Todaropsis* Girard, 1890, *Dosidicus* Steenstrup, 1857, *Hyaloteuthis* Gray, 1849, and *Euclidean* Berry, 1916. Vol II, P. 373-383. In: NA Voss *et al.* (eds), Systematics and Biogeography of Cephalopods. *Smithsonian Contributions to Zoology* 586. Vol. 1: 1-276; Vol. 2: 277-599. Washington D.C.
- Yamashiro C, L Mariátegui & A Taibe. 1997.** Cambios en la distribución y concentración del calamar gigante (*Dosidicus gigas*) frente a la costa peruana durante 1991-1995. Informe del Instituto del Mar del Perú-Callao 52: 1-40.
- Yamashiro C, L Mariátegui, J Rubio, J Argüelles, R Tafur, A Taibe & M Rabi. 1998.** Jumbo flying squid fishery in Perú. P. 89-105. In: T Okutani (ed). Contributed papers to international symposium on large pelagic squids, July 18-19, 1996. Japan Marine Fishery Research Centre (JAMARC), Tokyo, June 1998.