

Review

The biology and ecology of the jumbo squid *Dosidicus gigas* (Cephalopoda) in Chilean waters: a review

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ABSTRACT. The jumbo squid *Dosidicus gigas* is the most abundant cephalopod species in the southeastern Pacific Ocean, which supports the biggest cephalopod fishery in the world. Due to its growing economic importance, the population growth and distributional expansion of this squid is being increasingly studied. Nevertheless, some basic features of the biology of *D. gigas* are still unknown or have been poorly investigated. In this review we summarize the known information regarding the biology and ecology of this species in the southeastern Pacific Ocean; we focus on the Chilean region in order to propose hypotheses and research lines for a better understanding the life history of this organism. Available data on the size structure, reproduction and genetics of *D. gigas* allows us to propose hypotheses related to the squid's life history traits. Based on the current literature and publications of colleagues, we propose two hypotheses regarding the effect of spatial variation on the life history of *D. gigas*. Hypothesis 1: Squids mature at large sizes and spawn in oceanic waters with warm temperatures where paralarvae and juveniles develop. Immature squids migrate near shore to feed, grow and mature, and then return to the offshore sites to spawn. Hypothesis 2: Alternatively, juvenile *D. gigas* in the oceanic zone do not migrate to coastal waters and mature at small sizes compared to individuals living near the coast that mature at larger size and migrate to oceanic waters to spawn. We provide background information about the feeding behavior and parasitism of this species, suggesting that *D. gigas* is an important trophic link in the southeastern Pacific marine ecosystem. However, more studies on the feeding habits, reproduction and parasite load are needed not only to test hypotheses proposed in this study, but also to advance the overall knowledge of this species.

Keywords: *Dosidicus gigas*, squids, reproduction, feeding, life history, Chile.

Biología y ecología del calamar *Dosidicus gigas* (Cephalopoda) en aguas chilenas: una revisión

RESUMEN. *Dosidicus gigas*, es el calamar más abundante en el Pacífico suroriental, manteniendo la mayor pesquería mundial de cefalópodos. Su creciente importancia económica, ha motivado el aumento de estudios asociados al crecimiento de sus poblaciones y su expansión geográfica. Sin embargo, algunas características biológicas básicas de esta especie son desconocidas o escasamente estudiadas. En esta revisión, se resume la información sobre la biología y ecología de esta especie para el Pacífico suroriental y se proponen hipótesis y líneas de investigación para el mejor entendimiento de su historia de vida. Los datos sobre estructura de tamaños, reproducción y aspectos genéticos de la especie, permiten avanzar en las hipótesis relacionadas con la historia de vida de estos rasgos. Hipótesis 1: Los calamares maduran a gran tamaño y desovan en aguas oceánicas con temperaturas cálidas, donde paralarvas y juveniles se desarrollan. Los calamares inmaduros migran hacia la costa para alimentarse, crecer y madurar, y luego vuelven a los sitios en alta mar para desovar. Hipótesis 2: Alternativamente, los juveniles de *D. gigas* en la zona oceánica no migran a las aguas costeras y maduran peque-

ños en comparación a los individuos que viven cerca de la costa que maduran a un tamaño más grande y migran a las aguas oceánicas para desovar. Se proponen dos hipótesis acerca de la variación espacial de la historia de vida. Además, se proporciona el marco relativo a la alimentación y parasitismo del calamar, que coloca a *D. gigas* como un importante nexo trófico en los ecosistemas marinos del Pacífico suroriental. No obstante, se necesitan más estudios relacionados con alimentación, reproducción y carga parasitaria del calamar para poner a prueba las hipótesis propuestas en este trabajo.

Palabras clave: *Dosidicus gigas*, calamares, reproducción, alimentación, historia de vida, Chile.

INTRODUCTION

Dosidicus gigas (d'Orbigny, 1835), commonly known as the jumbo squid or Humboldt squid, is an ommastrephid squid species that can reach up to 1.2 m mantle length and 3.0 m total length (Fig. 1). *D. gigas* varies in body size and exhibits sexual dimorphism, high fertility, high voracity and a variable sex ratio (Markaida, 2001; Tafur *et al.*, 2010). This squid is the largest and most abundant (Nesis, 1970; Anderson & Rodhouse, 2001; Nigmatullin *et al.*, 2001) marine invertebrate of the fauna of the southeastern Pacific (Schmiede & Acuña, 1992; Fernández & Vásquez, 1995). *D. gigas* is ecologically distinguished from other ommastrephids by its wide latitudinal geographic range (Nigmatullin *et al.*, 2001); it has been suggested that its distribution limits could expand to Alaska and 45°S in the southeastern Pacific Ocean (Field *et al.*, 2007; Keyl *et al.*, 2008). *D. gigas* is an epipelagic and mesopelagic species inhabiting oceanic and neritic waters from the sea surface to 1,200 m depth (Nesis, 1970; Nigmatullin *et al.*, 2001).

Particularly due to the wide distribution (>10,000 km) of this species and the broad range of ecological conditions that it inhabits, *D. gigas* is an important model to study different aspects of biology in the fields of ecology and evolution. Here we summarized the existing biological and ecological information on *D. gigas*, including work published in Spanish and that is not yet fully digitized. Many of these sources of information in Latin America have been published as “gray literature” (*i.e.*, university theses and technical reports of national fishing institutes). The present review provides yet unpublished data on the distribution of paralarvae off the coast of Chile as well as information pertaining to the spatial variation in life history traits. Finally, this review provides background information about the feeding and parasitism of this species and a hypothesis is presented suggesting that *D. gigas* is an important trophic link in the southeastern Pacific marine ecosystem.

A brief history of early research (18th to 20th centuries)

First records of *D. gigas*, in Chilean waters and in the entire South American Pacific coastal waters, were re-

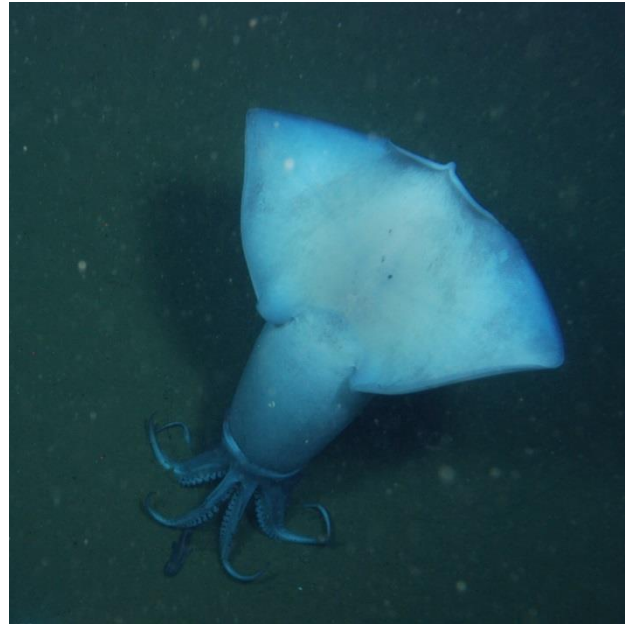


Figure 1. Specimen of the jumbo squid *Dosidicus gigas* catching a fish near Isla Mocha in spring 2010. Total length = 2.5 m. Image taken by ROV Kiel 6000 team, Chiflux cruise R/V Sonne, GEOMAR, September 2010, Chile. Photograph courtesy: Javier Sellanes.

ported by Juan Ignacio Molina in the 18th century. However, in early accounts the jumbo squid was identified as belonging to the same genus as the European cuttlefish (*Sepia officinalis* Linnaeus, 1758), called *Sepia tunicata* Molina, 1782. Later, in the 19th century Alcides d'Orbigny changed the genus/species classification of the jumbo squid to *Loligo gigas* d'Orbigny, 1835 (for details regarding systematics see Nigmatullin *et al.*, 2001). Following this, the naturalist Claudio Gay collected some specimens for L. Hupé of the Museum of Natural History in Paris, who determined that this squid should not belong to the genera *Sepia* (Sepiidae) or *Loligo* (Loliginidae), but rather to the family Ommastrephidae d'Orbigny, 1835 (for details see Schneider, 1930). Finally, in 1857, the Danish zoologist Johan Japetus Steenstrup proposed the genus *Dosidicus*, and the German zoologist George Pfeffer synonymized *D. eschrichtii* with *D. gigas* in 1912 (for details see Nigmatullin *et al.*, 2001).

During the first half of the 20th century massive strandings of *D. gigas* were reported off the Talcahuano coast around 37°S (Scheinder, 1930; Wilhelm, 1930, 1954) producing a nuisance to the local residents. These records of strandings boosted the study of the natural history of this squid for the first time, and begged biological hypotheses to explain this phenomenon. Ten years later, García-Tello (1964, 1965) published observations on squid bioluminescence and beak morphometry.

Between 1960 and 1970 researchers from the Universidad de Chile studied the giant axon of a *D. gigas* individual collected near Valparaiso (33°S) (see Schmiede & Acuña, 1992). Osorio *et al.* (1979) published an article regarding the economic importance of mollusks in Chile, highlighting four species of cephalopods: *Dosidicus gigas*, *Doryteuthis gahi* (d'Orbigny, 1835), *Octopus mimus* Gould, 1852 and *Robsonella fontaniana* (d'Orbigny, 1834); there were only fishing records for *D. gigas*. After 1978, *D. gigas* disappeared from Chilean coastal waters for 12 years, possibly due to environmental fluctuations caused by the El Niño events of 1982-1983 (Rocha & Vega, 2003). In the 1990's *D. gigas* returned to the Chilean coast (Schmiede & Acuña, 1992) supporting the local fishery in the Coquimbo region (30°S), although squid catches were described as ephemeral due to short periods of great abundance followed by periods where populations disappeared for several years (Fernández & Vásquez, 1995). After the El Niño events of 1997-1998, *D. gigas* disappeared from Chilean waters again (Rocha & Vega, 2003). Since 2001 *D. gigas* has been constantly present in increasing abundance in Chilean coastal waters, which has led to a renewed effort to investigate this ommastrephid cephalopod with emphasis on studying its biology and ecology. This research is detailed in the following specific sections.

Size structure of the jumbo squid

The size structure of *D. gigas* is multimodal, varying both spatially and temporally (Nigmatullin *et al.*, 2001; Chong *et al.*, 2005; Ibáñez & Cubillos, 2007; Keyl *et al.*, 2008; Liu *et al.*, 2010; Chen *et al.*, 2011). Several authors have indicated the possibility that groups of squids that mature at different sizes represent genetically discrete units, even at the sub-population or sub-specific level (Nesis, 1983; Argüelles *et al.*, 2001; Nigmatullin *et al.*, 2001). However, molecular studies performed using specimens of different stages of sexual maturity collected from Peru and Mexico have demonstrated that these phenotypes are not genetically different (Sandoval-Castellanos *et al.*, 2009) and only represent the large phenotypic flexibility of this species (Hoving *et al.*, 2013).

In coastal zones (<5 nm) offshore from Coquimbo (~30°S), mature large squids (>80 cm mantle length, ML) and pre-mature medium squids (<60 cm ML) were collected during the winter and spring of 1993 and 1994, respectively (Fernández & Vásquez, 1995; Chong *et al.*, 2005). Likewise, it was found that off the coast of Talcahuano (~37°S) during the years 2003 and 2004 the size structure of *D. gigas* populations changed between seasons. Medium-sized specimens were found in the oceanic zone and large specimens with a high ratio of maturity were found in the coastal zone during winter. During spring medium-sized adolescent and large mature specimens were found in the oceanic zone, while small immature and large mature specimens were found close to the coast. In summer only small immature and medium-sized adolescent specimens have been recorded near the shore (Ibáñez & Cubillos, 2007). Close to the coast of Coquimbo, large specimens (65-100 cm ML) were frequently found during the entire years of 2004 and 2005, while small specimens (45-55 cm ML) were only recorded during April and May (Arancibia *et al.*, 2007). Moreover, in coastal waters near Talcahuano (2004 and 2005), a modal progression of size structure was observed from winter to summer, which was dominated by large specimens (65-100 cm ML) and from summer to winter (*i.e.*, from December to August) by small specimens (25-45 cm ML) (Arancibia *et al.*, 2007). In international waters outside the Chilean Exclusive Economic Zone (hereafter EEZ) the size of *D. gigas* ranged from 20.6 to 70.2 cm ML both in spring 2007 and autumn 2008 (Chen *et al.*, 2011). In this context, several authors have suggested that the size structure of *D. gigas* found off the Chilean coastal is the result of a migratory pattern of jumbo squid from and to oceanic and coastal areas (Nesis, 1970; Ibáñez & Cubillos, 2007).

Age and growth of the jumbo squid

The age of cephalopods can be estimated by counting accretions in hard structures such as statoliths, beaks, and-in many decapod squids-gladii. However, the exact mechanisms of accretion can be complex and can depend on extrinsic factors such as temperature, oxygen level, and food availability (Keyl *et al.*, 2011). The statolith is the hard structure most often used for aging cephalopods. However, the basic assumption of "one mark, one day" is not valid for all species (Keyl *et al.*, 2011; Arkhipkin & Shcherbich, 2012). Until today it has not been possible to estimate the age and growth of *D. gigas*, mainly due to its very large and mobile nature. Because of this, there are no reported long-term laboratory experiments for this species. Nevertheless, statolith ring counting has been widely used for aging *D. gigas*. Often with this method, assuming daily

increments in the growth of statolith rings, the age of *D. gigas* individuals collected off the Chilean coast has been estimated to be one year or less (Liu *et al.*, 2010; Chen *et al.*, 2011). However, and contrary to the maximum number of around 450 marks which have been found, it is thought that individuals over 75 cm ML could live for 1.5 to 2 years (Liu *et al.*, 2010). The first known growth study based on modal progression analysis even found ages of 3 to 4 years for specimens larger than 50 cm (Nesis, 1970). A more recent modified modal progression analysis has estimated ages of up to 32 months for individuals collected off the coast of Peru (Keyl *et al.*, 2011). Moreover, a new report using a new technique for counting statolith rings reported a maximum of 832 rings in large specimens (1010 cm ML) collected in Peruvian waters (Arkhipkin *et al.*, 2015).

Genetic studies of the jumbo squid

Phylogenetic studies of mitochondrial DNA have confirmed that the jumbo squid *Dosidicus gigas* belongs to the subfamily Ommastrephinae (Wakabayashi *et al.*, 2006, 2012). Studies at the intra-specific level suggest that there are two genetic units, one in the Northern Hemisphere (Mexico-USA) and the other in the Southern Hemisphere (Peru-Chile), which are explained by the isolation by distance model (Sandoval-Castellanos *et al.*, 2007, 2010; Staaf *et al.*, 2010). Some studies using the Cytochrome b mitochondrial gene (Cyt b) and RAPDs have found genetic differences between squids caught in Peru versus those caught in Chile (Sandoval-Castellanos *et al.*, 2007, 2010). Conversely, using sequences of the Cytochrome Oxidase I mitochondrial gene (COI) there is evidence of high gene flow between populations in Chile and Peru (Ibáñez *et al.*, 2011; Ibáñez & Poulin, 2014). All studies thus far conducted are consistent in the sense that low overall genetic diversity was found, giving evidence to suggest that there has been a demographic expansion between the last glacial period and the present interglacial (Sandoval-Castellanos *et al.*, 2010; Ibáñez *et al.*, 2011). The historical fluctuations in the distribution range and population size of jumbo squid populations may be related to historical variation in productivity along the Humboldt Current System (HCS) (Ibáñez *et al.*, 2011; Ibáñez & Poulin, 2014). Overall, these studies indicate that *D. gigas* is a species characterized by high vagility during its different ontogenetic states (*e.g.*, egg masses, paralarvae and adults) and is potentially an ecological opportunist. Assuming that *D. gigas* achieves a maximum age of more than two years, it can be expected that ontogenetic migrations (both vertical and horizontal) are possible, even across thousands of km.

Reproduction of the jumbo squid

The reproductive strategy of *D. gigas* involves multiple spawning (Rocha *et al.*, 2001). The spawning is monocyclic, yielding a high fertility potential (~32 million eggs). Egg laying occurs in a separate phase and there is somatic growth between spawning events (Rocha *et al.*, 2001; Nigmatullin & Markaida, 2009). Males (>65 cm ML) become sexually mature before females (>70 cm ML) (Nesis, 1970; Markaida & Sosa-Nishizaki, 2001; Ibáñez & Cubillos, 2007), which is a difference that has been described as a general feature of cephalopods (González & Guerra, 1996). However, a study utilizing specimens sampled in the EEZ off the coast of Chile showed that the composition of males and females at sexual maturity in the sample group was similar (Liu *et al.*, 2010) and the length of sexual maturity was 56.5 and 63.8 cm ML for males and females, respectively. Further north, the recorded length at maturity was less than that seen in *D. gigas* specimens collected further south. In addition, severe changes in length at maturity have been reported in the north. Until the 1997/1998 El Niño, length at maturity in Peruvian waters was less than 40 cm for females and even less for males. After the El Niño event, length at maturity more than doubled in 1 to 2 years (Argüelles *et al.*, 2008; Tafur *et al.*, 2010). However, length at maturity can be below 20 cm in the northern HCS (Rubio & Salazar, 1992). Size at maturity depends on temperature and food availability, meaning that jumbo squid will mature at smaller sizes under warm conditions (*e.g.*, El Niño) and at larger sizes in cool conditions, allowing longer migration distances (*e.g.*, La Niña) (Keyl *et al.*, 2008).

González & Chong (2006) examined 254 specimens (93 during winter and 161 during spring) collected off the coast of Coquimbo (~30°S) in 1993 and suggested based on histological evidence that reproduction is not seasonal, meaning that it is possible to find sexually mature specimens throughout the year. Similarly, in another study Nigmatullin *et al.* (2001) determined that spawning occurs throughout the year. However, other studies (*e.g.*, Clarke & Paliza, 2000; Arancibia *et al.*, 2007; Liu *et al.*, 2010) found evidence for two spawning groups (summer and winter). Likewise, Zúñiga *et al.* (2008) postulated the existence of two reproductive cycles, based on a regular periodicity pattern detected monthly during catches conducted between 2002 and 2005. Furthermore, the analysis of specimens caught in Peruvian waters found a “maturity baseline” with two spawning peaks (Tafur *et al.*, 2010).

Gonadosomatic index (GSI) analyses of *D. gigas* conducted between July 2003 and February 2004 indicated higher GSI measurements for males during October and for females during November because of

the later maturation of females (Cubillos *et al.*, 2004; Tafur *et al.*, 2010). However, no spawning evidence was found during winter and spring using macroscopic examination techniques and histological analysis of the gonads (Cubillos *et al.*, 2004; Gallardo, 2004). Analysis of the ratio of microelements deposited in statoliths can be useful to discriminate spawning seasons (*e.g.*, Mg:Ca and Sr:Ca, Liu *et al.*, 2011). The analysis of the Sr:Ca ratio of *D. gigas* collected in the EEZ in Chile and Peru led to the conclusion by some authors that there exist two spawning seasons (autumn and winter) (Liu *et al.*, 2011). However, Chen *et al.* (2011) using individuals hatched between January and December 2008 outside of the Chilean EEZ, suggested that *D. gigas* spawns throughout the year, with peaks in August and November (austral winter and spring respectively). Similar observations were made by Keyl *et al.* (2011) using samples collected inside the Peruvian EEZ. Thus evidence from different studies reveals that mature specimens of *D. gigas* may spawn throughout the year in offshore zones (*i.e.*, oceanic waters in EEZ), with two periods of maximum reproductive activity in winter and summer. Spawning also occurs in oceanic waters, as *D. gigas* paralarvae have been collected off the Chilean coast (Nesis, 1970; this study, Table 1 and Fig. 2), in Peruvian waters and in the Equatorial zone (Sakai & Yamashiro, 2013; Staff *et al.*, 2013). While studies on the fecundity of *D. gigas* are insufficient, one author found that individual females in Chile could produce approximately 312,612 eggs (Gallardo, 2004). In the same study, Gallardo (2004) reported that the size of ripe eggs ranged from 0.76-2.28 mm.

The feeding of the jumbo squid

The jumbo squid is a non-selective predator with a wide trophic niche and a high consumption rate (Ibáñez, 2013). The first diet records of *D. gigas* in Chile were made by Schneider (1930) and Wilhelm (1930, 1954) who studied the stomach contents of stranded squids on Bahía Concepción beaches. In these observations remains of sardine *Sardinops sagax* (Jenyns, 1842), hake *Merluccius gayi* (Guichenot, 1848), conger eels *Genypterus chilensis* (Guichenot, 1848) and *G. blacodes* (Forster, 1801), ghost shrimp *Neotrypaea uncinata* (H. Milne-Edwards, 1837) and *Pseudosquilla lessonii* (Guérin, 1830) and the crabs *Paraxanthus* sp. and *Epialtus* sp. were found. In addition, unidentified small mollusks were found in the gut contents, as was the first evidence of cannibalism. Several decades later in the 1990s, when *D. gigas* was again abundant off the Chilean coast, the jack mackerel *Trachurus murphyi* (Nichols, 1920) was newly recorded, as was a high degree of cannibalism (Fernández & Vásquez, 1995). From 1993 the 1994 the recorded prey species composition was similar to that

Table 1. Data of *Dosidicus gigas* paralarvae collected off the coast of Central Chile during November 11-14, 2003 during the FIP 2002-12 cruises. All paralarvae were identified and measured by C.M. Ibáñez. ID: Station number.

ID	Mantle length (mm)	Temperature (°C)	Hour
1	2.0	15.5	4:25
2	1.2	16.1	1:35
3	1.5	15.8	7:52
4	1.5	13.5	0:38
5	2.5	13.7	6:40
6	2.8	14.7	16:02
7	1.2	14.8	11:50
8	3.1	16.4	21:25
9	2.5	15.3	18:42
10	3.5	15.5	11:37
11	2.0	15.6	2:00
12	2.2	16.6	7:36
13	4.0	16.3	12:55
14	1.7	15.9	5:28
15	1.5	16.3	1:50
16	1.5	16.1	21:39

described above, though it also included myctophid fishes, *Engraulis ringens* Delfin, 1901, amphipods and euphausiids (Chong *et al.*, 2005). More recently, Liu *et al.* (2010) determined the existence of three main groups of prey organisms in the EEZ: lantern fish, cephalopods (including cannibalism) and crustaceans.

During the last period of high abundance of jumbo squid from 2001 to 2010, an analysis of stomach contents of *D. gigas* taken in hake fishing was performed and a high occurrence of hakes in the diet of squid was found (40%; Ulloa *et al.*, 2006). This finding confirmed that hake was decreasing in abundance due to jumbo squid predation, which led to the beginning of a controversial discussion (Ibáñez, 2013). A study on *D. gigas* caught using different sampling gear (purse seine, trawl and jigs) in different fisheries (hake, jack mackerel, hoki, sardine and jumbo squid) found a bias in the stomach content of the squid according to the fishing target and gear. Jumbo squid stomach content samples from the hake fishery showed 100% *M. gayi*, while samples from mackerel fishery showed 98% *T. murphyi* (Ibáñez *et al.*, 2008). The same bias occurs with cannibalism in different regions (Ibáñez & Keyl, 2010).

The majority of the feeding records of *D. gigas* are descriptive (Fernández & Vásquez, 1995; Ibáñez *et al.*, 2008). Few studies have found that *D. gigas* collected off the Chilean coast do not show feeding differences

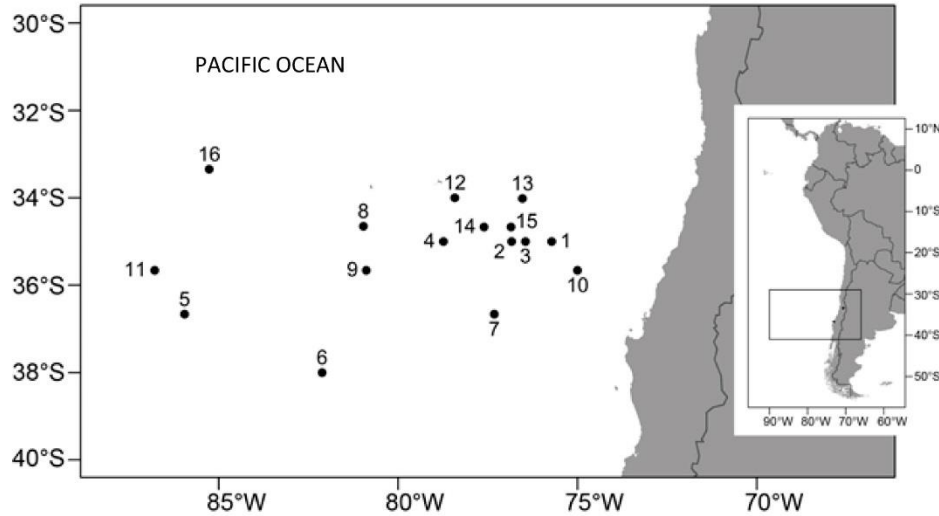


Figure 2. Sampling stations where paralarvae of *Dosidicus gigas* were captured during the project FIP 2002-12, November 11-14, 2003. For details, see Table 1.

related to their sexual and ontogenetic condition (Ulloa *et al.*, 2006, 2012; Pardo-Gandarillas *et al.*, 2014). Apparently, variability in stomach contents occurs on a seasonal and geographic scale, possibly due to changes in prey availability in the HCS ecosystem (Chong *et al.*, 2005; Pardo-Gandarillas *et al.*, 2014).

It is estimated that individual jumbo squid can consume between 100 and 901 g day⁻¹ of food. This is equivalent to 1.4-4.1% of the weight of the predator (Cubillos *et al.*, 2004; Arancibia *et al.*, 2007). All these analyses are based on the measured stomach contents, because squid do not accept food when kept in enclosures (Arancibia *et al.*, 2007). Some other studies that have been conducted to measure the consumption/biomass ratios of jumbo squid have been shown to be biased (for details see Ibáñez, 2013).

Dietary studies using stable isotopes in *D. gigas* collected from Chilean waters showed interesting results. Both the ¹³C and ¹⁵N levels were higher in the Chilean coast than in the rest of their geographic range (Ruiz-Coolley & Gerrodette, 2012). This implies that *D. gigas* has a high trophic level consequence on its prey, and also that the squid's prey in Chilean waters has a higher trophic level.

Predators of the jumbo squid

Sperm whales (Clarke & Paliza, 2001), sharks (López *et al.*, 2009, 2010) and swordfish (Ibáñez *et al.*, 2004; Castillo *et al.*, 2007; Letelier *et al.*, 2009) are the main predators of *D. gigas* found in Chilean coastal waters. In the Eastern Pacific, the diet of sperm whale populations consists of 100% jumbo squid (Clarke *et*

al., 1988; Clarke & Paliza, 2001). In food webs, *D. gigas* is assumed to have a trophic level around 4.0 (Ibáñez, 2013). In this scenario, the trophic position of *D. gigas* occupies an intermediate to high level (Fig. 3).

Parasites of the jumbo squid

Pardo-Gandarillas *et al.* (2009) described and quantified the parasitic fauna associated with *D. gigas* caught in oceanic and coastal waters in Central Chile (32°S-40°S). 97% of the specimens showed infestation of cestode larvae: *Hepatoxylon trichiuri* (Holten, 1802) (abundance of 2.6 and prevalence of 70.2%), *Tentacularia coryphaenae* Bosc, 1802 (0.1 abundance, 5.6% prevalence), plerocercoid Tetracystidae (9.1 abundance, 83.1% prevalence), *Pelichnibothrium speciosum* Monticelli, 1889, *Anisakis* Type I (0.06 abundance, 6.5% prevalence) and *Anisakis* type II (0.52 abundance, 17.7% prevalence). Among the parasite species mentioned, *H. trichiuri* is a newly recorded parasite of *D. gigas* in the latitudes of the southeastern Pacific. Other taxa were previously described for *D. gigas* inhabiting Ecuador, Peru, and northern Chile (Shukhgalter & Nigmatullin, 2001). However, genetic studies have been suggested to identify larval nematodes associated with the jumbo squid as there is limited information about these taxa and they are difficult to identify visually (Pardo-Gandarillas *et al.*, 2009). The composition and abundance of the parasite communities of *D. gigas* are different between oceanic and coastal waters off of Chile, which could be explained by the type of diet of *D. gigas* in each zone (Pardo-Gandarillas *et al.*, 2014). Species richness, relative abundance and diversity of parasites increase in

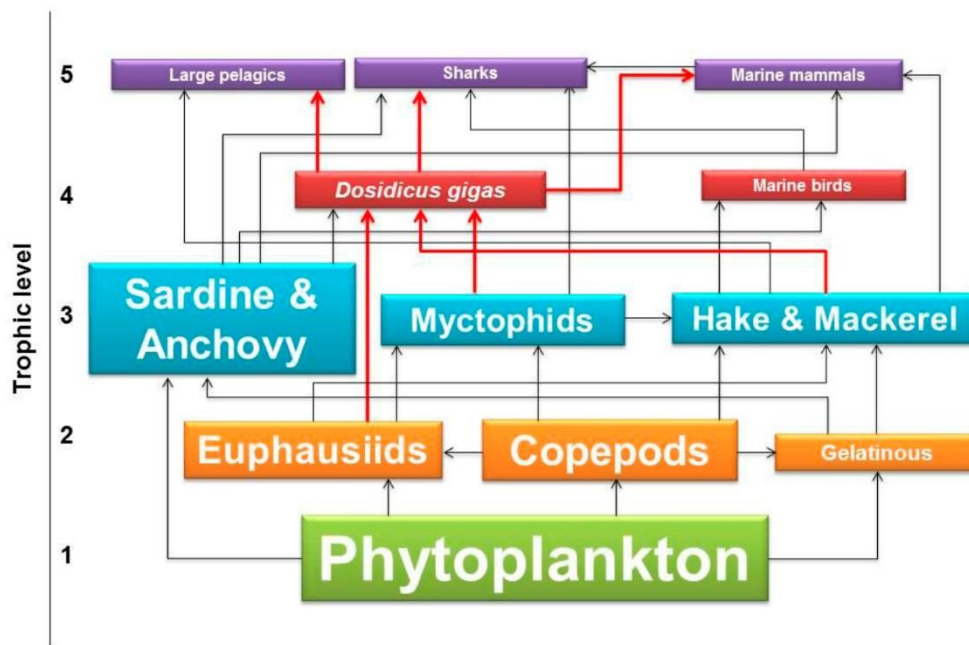


Figure 3. Trophic and parasite network. Black lines indicate trophic dynamics and red lines indicate parasite dynamics. Redrawn from Ibáñez (2013). The size of each box represents the relative biomass.

relation to squid size due to the aggregation and accumulation of parasites over time in the host (Pardo-Gandarillas *et al.*, 2014). Squids can act as parathenic hosts (*i.e.*, intermediate), thereby maintaining the life cycles of the parasites. These life cycles are then completed when the parasite is transferred to large predators of *D. gigas* (definitive host) such as sharks and sperm whales (Fig. 3).

FINAL REMARKS

In the last 15 years, the number of studies on the jumbo squid *D. gigas* has significantly increased in Chile and elsewhere; these new studies have covered biological, ecological, genetic and fisheries themes. Despite this growing information we still do not know much about the basic biology of this species in Chile or elsewhere. The information collected in this study allows us to formulate some hypotheses and lines of research for future studies of the jumbo squid. This can help researchers to continue learning about this species, which is an excellent model for posing questions about more general aspects of biology.

Spatial and temporal differences in water temperature and food abundance have been proposed to explain changes in maturation, growth and migration of *D. gigas* in Peruvian waters (Keyl *et al.*, 2008). In line with this, we propose two hypotheses (scenario 1 and 2) to explain the patterns reported of the life history of *D. gigas* inhabiting Chilean waters. We make these hypotheses based on published information on the size structure, stage of maturation and paralarvae distribution of *D. gigas*, assuming that in Chilean waters the

squid is reproducing year-round and has two pronounced spawning peaks (winter and summer) that occur in oceanic zones (Clarke & Paliza, 2000; González & Chong, 2006; Zúñiga *et al.*, 2008; Liu *et al.*, 2010).

Hypothesis 1: Squids mature at large sizes and spawn in oceanic waters with warm temperatures where paralarvae and juveniles (<10 mm ML) develop. Generally, it is assumed that the immature squids (<200 mm ML) migrate near shore to feed, grow and mature at large sizes (>700 mm ML), and then return to the offshore sites in order to spawn (see Fig. 4a, Scenario 1). During these ontogenetic migrations from oceanic to coastal waters and vice versa, the squids change their diet (Nesis, 1970; Pardo-Gandarillas *et al.*, 2014). A similar conceptual model has been proposed in Peruvian waters; where squids migrate from coastal to oceanic waters and in doing so, change their prey preferences (Alegre *et al.*, 2014). In the same way, Arkhipkin (2013) proposed that *D. gigas* utilizes the high productivity waters of the continental slope during spawning migrations to the open ocean.

Hypothesis 2: Alternatively, juvenile *D. gigas* in the oceanic zone off Chilean HCS do not migrate to coastal waters and mature at small sizes (56–63 cm ML; Liu *et al.*, 2010, see Fig. 4b, Scenario 2) compared to individuals living near the coast that mature at larger size (66–71 cm ML; Ibáñez & Cubillos, 2007) and migrate to oceanic waters to spawn. The mechanisms promoting such phenotypic variation (*e.g.*, size at maturity) are not well known, but without an evolutionary

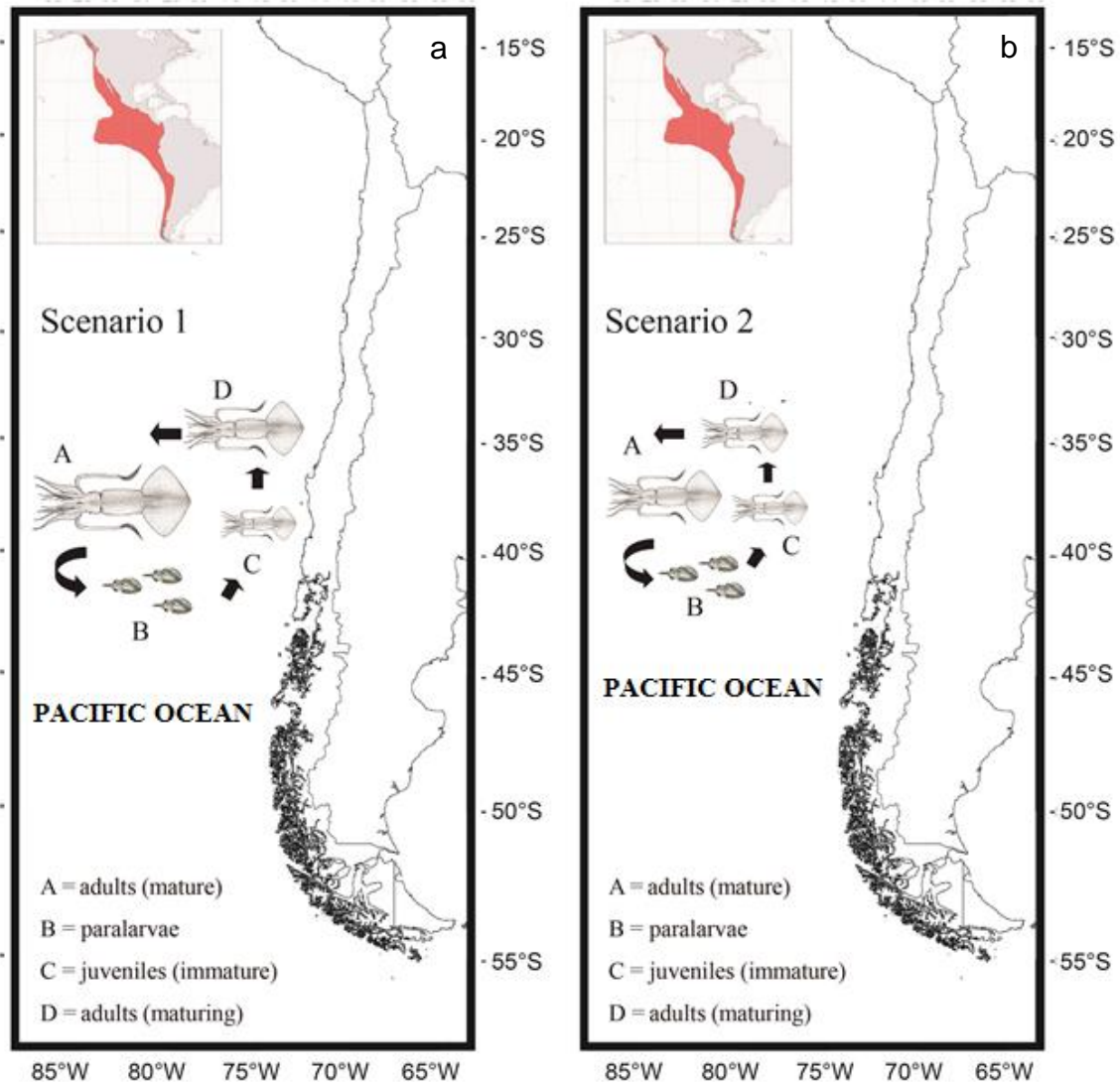


Figure 4. Hypotheses of the life-history characteristics of *Dosidicus gigas* in Chilean coastal waters. a) Scenario 1: adult squids spawn in offshore oceanic waters and sub-adults return to near shore waters to feed, grow, and mature to larger sizes. b) Scenario 2: adult squids spawn and mature in offshore oceanic waters at small sizes.

perspective it is difficult to predict the biological response of marine populations to environmental changes (Munday *et al.*, 2013; Harvey *et al.*, 2014). From the evolutionary point of view, phenotypic plasticity and flexibility are commonly observed in temperate marine species, which experience a great range of temporal and spatial variation in temperatures (Piersma & Drent, 2003; Somero, 2005). On one hand, *D. gigas* inhabit a variable environment and they can exhibit considerable phenotypic plasticity in their size at maturity given the temporal and spatial scale (*e.g.*, Argüelles *et al.*, 2008; Keyl *et al.*, 2008; Hoving *et al.*, 2013). On the other hand, developmental plasticity, the environmentally induced variability experienced

during development within a single genotype (Piersma & Drent, 2003), has been recently given much attention. Epigenetic forces appear to be one central mechanism promoting developmental plasticity, as environmental factors such as temperature and nutrition have been shown to impact patterns of genome methylation in marine invertebrates, altering gene expression rates (Somero, 2005; Harvey *et al.*, 2014). In the case of *D. gigas*, the water temperature of the spawning area and the food quality for paralarvae could be important in determining the final size at maturity in different temporal and spatial scales. The size of hatchlings emerging from eggs is smaller with increased water temperature and when the adults are

younger when they reach maturity (Pecl & Jackson, 2008; Arkhipkin *et al.*, 2015). In fish, early influences (*e.g.*, temperature, food) on life history traits can be responsible for later life-history variation (*e.g.*, fecundity, size at maturity) (Jonsson & Jonsson, 2014).

Comparing the life history traits of *D. gigas* from Chile, Peru, and Mexico (Table 2), we did not find differences in the longevity or size at maturity. Regarding fecundity and egg size (Table 2), it is difficult to make a conclusion about differences between traits of *D. gigas* from the three different locations because there are an insufficient number of studies ($n < 5$), which have been conducted using different methodologies. However, we assume that the life history of *D. gigas* is plastic and altered by temporal environmental changes (*e.g.*, temperature, food) in the same way as in different ecosystems as suggested by Hoving *et al.* (2013).

D. gigas plays an important role in the HCS coastal and oceanic ecosystem as it consumes a wide variety of invertebrates and fishes, and it is important prey for other cephalopods, fishes, birds and marine mammals (Ibáñez, 2013). Like other squids, the jumbo squid is considered a nutrient vector linking spatially distinct marine ecosystems (Arkhipkin, 2013). Compared to other locations (*e.g.*, Peru and Mexico) the diet of *D. gigas* off Chile is not different in terms of functional or taxonomic groups. The jumbo squid mainly feeds on mesopelagic fishes, cephalopods and euphausiids in all of these geographic regions (Markaida & Soza-Nishizaki, 2003; Ibáñez *et al.*, 2008; Alegre *et al.*, 2014).

It is possible that, as for many cephalopods, *D. gigas* may be a trophic bridge for the vertical transmission of parasites between its prey (crustaceans and fishes) and predators (sperm whales, swordfish and sharks) (Abollo *et al.*, 1998; Pardo-Gandarillas *et al.*, 2009). It is not yet clear from whom *D. gigas* acquires these parasites. Nevertheless, it is likely that the squid ingests the parasites through its diet of euphausiids, myctophids, hake and jack mackerel (Fig. 3). Jumbo squid parasites collected from Chilean, Peruvian and Equatorial waters showed differences in the presence and absence of some taxa (Shukhgalter & Nigmatullin, 2001; Pardo-Gandarillas *et al.*, 2009; Céspedes *et al.*, 2011). However, most of these parasites have high rates of synonymy when identified by light microscopy, and molecular analysis is needed to improve robust identification of rare taxa (Pardo-Gandarillas *et al.*, 2009).

To understand fully the biology and ecology of *D. gigas* in Chilean waters from an evolutionary perspective, it is necessary to perform new phylogeographic studies of the Chilean-Peruvian population(s).

Furthermore, it is important to account for processes underlying patterns in the physical oceanography. For these future studies, it is necessary to incorporate variables related to adult migration, dispersal of egg masses and dispersal of paralarvae.

Future research on jumbo squids in Chilean waters should address the following:

1. Increase our knowledge on the diversity, structure and genetic characterization of *D. gigas* populations in the Peruvian-Chilean province using novel molecular markers (*e.g.*, microsatellites, SNPs). This information is important in order to establish conservation strategies conducive to population management in both Chile and Peru.
2. Incorporate satellite tagging of the Peruvian-Chilean populations, similar to studies conducted in the Northern Hemisphere (Gilly *et al.*, 2006; Bazzino *et al.*, 2010). This will help clarify an important part of *D. gigas*'s life cycle, such as rhythms and directionality of horizontal and vertical migrations.
3. Clarify the controversy about whether populations of *D. gigas* in Chile reproduce all year or whether there are certain periods where such events occur more frequently.
4. Implement a spatial and temporal monitoring system of *D. gigas* in Chile measuring growth, reproduction and feeding, among others.
5. Improve consumption estimations and perform feeding-related studies of *D. gigas* using various approaches (*e.g.*, stomach content, stable isotopes, lipids and DNA).
6. Perform genetic studies on the squid parasites to determine the taxonomic identity of the parasite species.
7. Determine the biological condition of squids and establish how they are impacted by environmental and ecological factors of their environment, especially during ENSO events.
8. Evaluate populations of *D. gigas* sampling their complete distribution and testing for potential phenotypic differences (*e.g.*, size at maturity). In addition, evaluate whether these differences are defined by geography (latitudinal change) or by environmental variation such as temperature, salinity, and/or productivity.
9. Standardize the different methods used to study *D. gigas* in Chilean waters in order to generate a framework including all relevant information about this species.
10. Estimate heritability of size at maturity in a microevolutionary context, and evaluate how natural selection drives changes in the size at maturity. Addi-

Table 2. Comparative data of *Dosidicus gigas* life history. ^aTafur *et al.* (2010); ^bChen *et al.* (2010); ^cArgüelles *et al.* (2001); ^dMarkaida (2001); ^eGallardo (2004); ^fNesis (1970). *Estimation based on one mature female.

Life history traits	Chile	Peru	Mexico
Size at maturity males (mm)	250 - 796 ^a	170 - 800 ^a	180 - 760 ^a
Size at maturity females (mm)	400 - 890 ^a	150 - 900 ^a	200 - 800 ^a
Longevity males (days)	127 - 302 ^b	120 - 325 ^c	367 - 372 ^d
Longevity females (days)	150 - 307 ^b	110 - 345 ^c	434 - 442 ^d
Fecundity males (spermatophores)	1,347 - 3,059 ^e	500 - 1,334 ^f	54 - 1,334 ^d
Fecundity females (eggs)	312,612 ^{e*}	100×10 ⁵ - 650×10 ⁵ ^f	5.2×10 ⁶ - 32×10 ⁶ ^d
Egg size (mm)	0.76 - 2.28 ^e	0.90 - 1.10 ^f	0.87 - 1.11 ^d

tionally, study the RNA/DNA ratios to evaluate different growth rates related to the hypotheses proposed.

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