SPRFMO

3rd Meeting of the Scientific Committee

Port Vila, Vanuatu
28 September - 3 October 2015

SC-03-27

Main Biological and fishery aspects of the Jumbo squid in the Peruvian Humboldt Current System

J. Csirke, A. Alegre, J. Argüelles, R. Guevara-Carrasco,
L. Mariátegui, M. Segura, R. Tafúr & C. Yamashiro

Main biological and fishery aspects of the jumbo squid (*Dosidicus gigas*) in the Peruvian Humboldt Current System

by
Jorge Csirke, Ana Alegre, Juan Argüelles, Renato Guevara-Carrasco, Luís Mariátegui, Marceliano Segura, Ricardo Tafúr and Cármen Yamashiro

Instituto del Mar del Perú (IMARPE), Chucuito, Callao, Perú

Summary

Jumbo squid (*Dosidicus gigas*) is found in high abundance along the whole Peruvian coast from 10 to more than 500 nm from the coast. Performs diel vertical migrations from 0 to more than 650 m depth, and regular inshore-offshore ontogenetic migrations and less regular latitudinal migrations of several hundred miles. Younger and/or smaller jumbo squids predominate in oceanic waters, while larger jumbo squids are more neritic. Maintains some reproductive activity all year round, with increased reproductive activity from July to February and peaks between October and January. Life span is usually one year, although some specimens can live up to two years. Slight differences in the age or size of sexual maturity and main distribution areas suggests that there are least three strains, groups or population subunits of jumbo squid inhabiting the Peruvian Humboldt Current System. Is a very aggressive predator and prey availability seems to be more important than temperature or other environmental parameters in shaping its geographic distribution. Has a wide food spectrum, mostly feeding on cephalopods (26.4%, by weight) and mesopelagic fish *Vinciguerria lucetia* (24.4%) and Myctophidae (18.3%). The development of the jumbo squid fishery in Peru is characterized an initial rapid development in the early 1990s of a licensed foreign industrial fishery and a local artisanal fishery that gradually has phased out of the industrial fishery. Total catches of jumbo squid in Peruvian jurisdictional waters peak at 559,000 t in 2008, with a total of 506,000 t in 2014, all taken by the local artisanal fleet. The size frequency distribution of jumbo squid in both the artisanal and the industrial fishery has been highly variable with a significant shift in 2000. From 1989 to 1999 most jumbo squid was under 50 cm ML, with one or two modes between 20 and 40 cm ML; while since 2000 there is a prevalence of jumbo squid larger than 50 cm ML, with 2 or 3 modes between 22 cm and 93 cm ML. Since 1999 the assessments of jumbo squid in Peruvian waters has been based predominantly on the biomass estimates obtained through hydro-acoustic surveys and more recently, as longer CPUE time series were available these assessments have also included the application of a surplus production model. Both assessment methods have provided estimates that are compatible with the high current catches and an under-exploited state of exploitation.

1. Introduction

Jumbo squid (*Dosidicus gigas*) is one of the largest and the most abundant cephalopod species of the world. Since 2008 is the single cephalopod species yielding the highest total annual catch worldwide, with a maximum of 951,000 t in 2012. Is only found in the Eastern Pacific Ocean, where it has a wide neritic-oceanic distribution along the edges of the highly productive coastal upwelling areas from the 35°N to 55°S. Is particularly abundant where the surface oxygen saturation is relatively high and there are high concentrations of mesopelagic species which form important part of their diet (Nesis, 1970,1983; Roper et al., 1984; Nigmatullin *et al*., 2001; Ehrhardt *et al*., 1983; Kreuser, 1984; Markaida 2006; Rosas, 2007, Rosas *et al*., 2011; Seibel, 2011, 2013; Alegre, 2014). The areas with the highest concentrations of jumbo squid are associated with the upwelling systems of the northern-central zone of Peru and the Gulf of California (Anderson and Rodhouse, 2001; Arguelles *et al*., 2001; Markaida and Sosa-Nishizaki, 2003; Nigmatullin *et al*., 2001), which also sustain the largest fisheries for this species.

As other squid species, jumbo squid is fast growing, short-lived and the population is usually composed of individuals from a single year-class. This causes their abundance and distribution patterns to be very sensitive to changes in the environmental conditions and the effects on the abundance of their prey (Bazzino 2001). The environmental effects on the production cycle of zooplankton appear to be particularly important since zooplankton is the main food source of juvenile jumbo squids.

Prior to 1989 Peru was landing well under 1,000 t of jumbo squid per year, all coming from incidental catches (Flores *et al*., 1994). A directed fishery for this species in Peruvian jurisdictional waters started between 1990 and 1991 with an increased effort and catches by local artisanal vessels, and the licensing of a limited number of foreign industrial jigger vessels. The Peruvian artisanal fleet caught almost 21,000 t of jumbo squid in 1991 and 43,000 t in 1994, while as of April 1991 the Peruvian Government granted fishing licenses to a limited number of foreign industrial jigger vessels that caught almost 61,000 t of jumbo squid in 1991 and 170,000 t in 1994. These licenses were granted after large concentrations of jumbo squid were found in Peruvian and adjacent high-sea waters by scientific and exploratory fishing surveys conducted in 1989 and 1990.

As part of the management of this developing fishery a research and monitoring program was established, which included dedicated observers on board and in the main landing sites combined with sea-going scientific surveys covering Peruvian jurisdictional waters as well as the adjacent high seas. This active research and monitoring program continues to-date, albeit with some adjustments and modifications, while the industrial fishery for jumbo squid in Peruvian jurisdictional waters has been phased-out almost completely by the expansion of the local artisanal fishery that now has some 2,350 vessels with average hold capacity of 9.8 t and is now catching around 500,000 t of jumbo squid a year.

The ongoing research on this species has shown that the behavior and distribution patterns as well as the levels of biomass, body size and time or age at sexual maturity of jumbo squid are often modified during intense events of El Niño or La Niña, where from the fisheries perspective the most noticeable effects are the increased dispersion and reduced accessibility of jumbo squid to the fishing fleets (Arguelles , *et al*., 2008; Arguelles and Tafur, 2010). These and other aspects of the biology, ecology and fishery of the jumbo squid (*D. gigas*) in Peruvian jurisdictional waters and in the adjacent high seas are briefly described below, including notes on its distribution, habitat, migrations patterns, reproduction, age and growth, trophic interactions, population structure, population size, fishery and fisheries management.

2. Horizontal and vertical distribution

Jumbo squid is commonly found along the whole Peruvian coast occupying areas at 10 to more than 500 nm from the coast and depending on the time of day, from the surface to depths of 600 m or more. Stock size, local abundances and depths, latitudes and distances from the coast at which the highest concentrations occur may vary greatly, seasonally and from year to year. Nevertheless, the highest abundances and best concentrations of commercial importance usually occur off the northern and central part of the Peruvian coast and within 10 to 50 nm from the coast in summer and 40 to 90 nm in winter and spring.

Valuable information on the horizontal and vertical distribution of jumbo squid and its variability with time is obtained from the records and observations of the industrial and local artisanal fisheries, as well as from the scientific surveys conducted by IMARPE. Acoustic surveys covering a wide coastal area (typically from 10 to 100 nm from the coast) conducted by IMARPE since 1999 confirm the conspicuous presence and wide distribution of jumbo squid along the whole Peruvian coast. These surveys also show that there is a high seasonal and yearly variability in the distribution and extension of the areas with

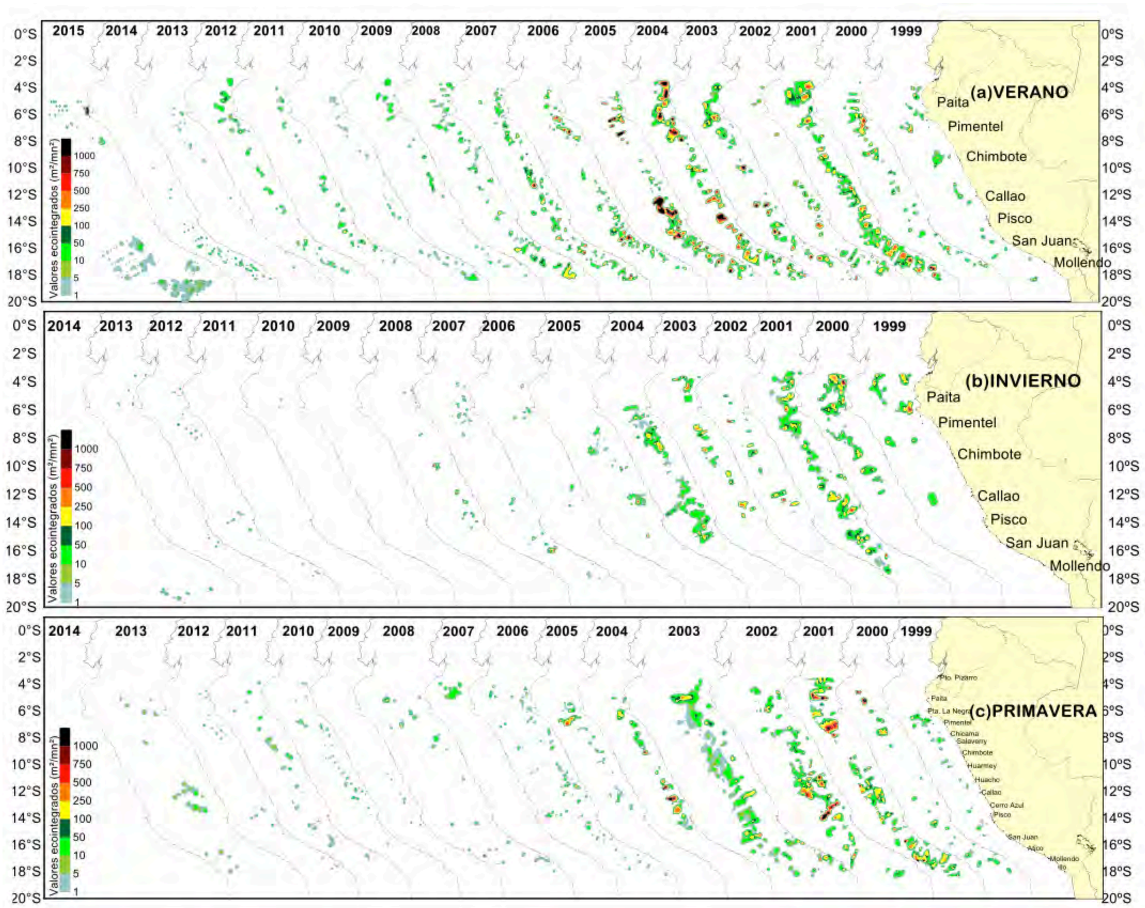

Figure 1.- Horizontal distribution of jumbo squid (*D. gigas*) concentrations during acoustic scientific surveys conducted by IMARPE along the Peruvian coast during: (a) summer; (b) winter; and, (c) spring. Years 1999 to 2015.

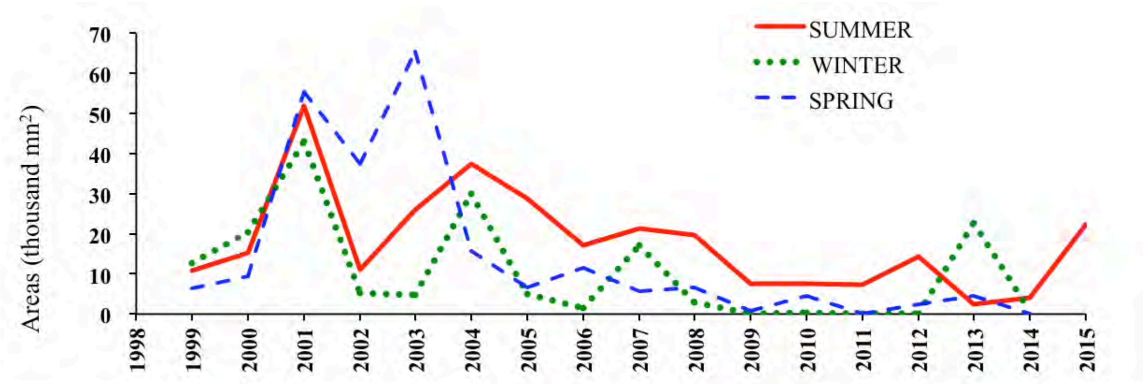

Figure 2.- Distribution areas of jumbo squid (*D. gigas*) within the coastal areas covered by IMARPE scientific acoustic surveys, by season and years, from 1999 to 2012.

jumbo squid within the coastal band surveyed, within which jumbo squid is generally more widely distributed during spring and summer (Figures 1 and 2)(autumn is not shown due to low number of autumn surveys).

Between 2001 and 2008 jumbo squid occupied a larger portion of the coastal band being surveyed. This is more noticeable for the summer months where jumbo squid had a wider, more dispersed distribution within the coastal area surveyed, with maximums in 2001 and 2004. Then, after 2009 jumbo squid was more concentrated in fewer, smaller higher density 'pockets' within the surveyed area, except for summer 2012 that had more jumbo squid within the surveyed area, and for the survey in summer 2015 that had a different area coverage, focusing more on the current main fishing areas in the north and in the south, to as far as 200 nm from the coast.

The coastal areas occupied by jumbo squid during winter were also highly variable with some larger values in 2001, 2004, 2007 and 2013. Since 2008 there is a predominance of lower values, suggesting that jumbo squid had a more oceanic winter distribution, beyond the surveyed area. During the spring months between 1999 and 2004 jumbo squid appears again occupying larger portions of the coastal area being surveyed, with maximums in 2001 and 2003, while from 2005 to 2014 was also found in fewer, smaller, concentrated 'pockets' within the surveyed area.

The inshore-offshore location of the centers of gravity of the acoustic abundance indexes by season and year between 1999 and 2012 also show a consistent more coastal distribution of jumbo squid during summer, with noticeable yearly variability in their proximity to the coast in all seasons (Figure 3). It is noted that except for the summers of 1999 and 2000 when these centers of higher abundance were located respectively at 74 and 61 nm from the coast, during summer these centers of gravity of higher abundance have been within 50 nm from the coast, getting as close as 14 and 18 nm from the coast in 2002 and 2008. While except for a couple of winters in 2005 and 2008 and spring in 2004, 2011 and 2012, these centers of gravity have been outside the 50 nm from the coast in winter and spring. It is worth noting that the wider offshore distribution observed during the summers of 1999 and 2000 were dominated by colder than normal 'La Niña' conditions.

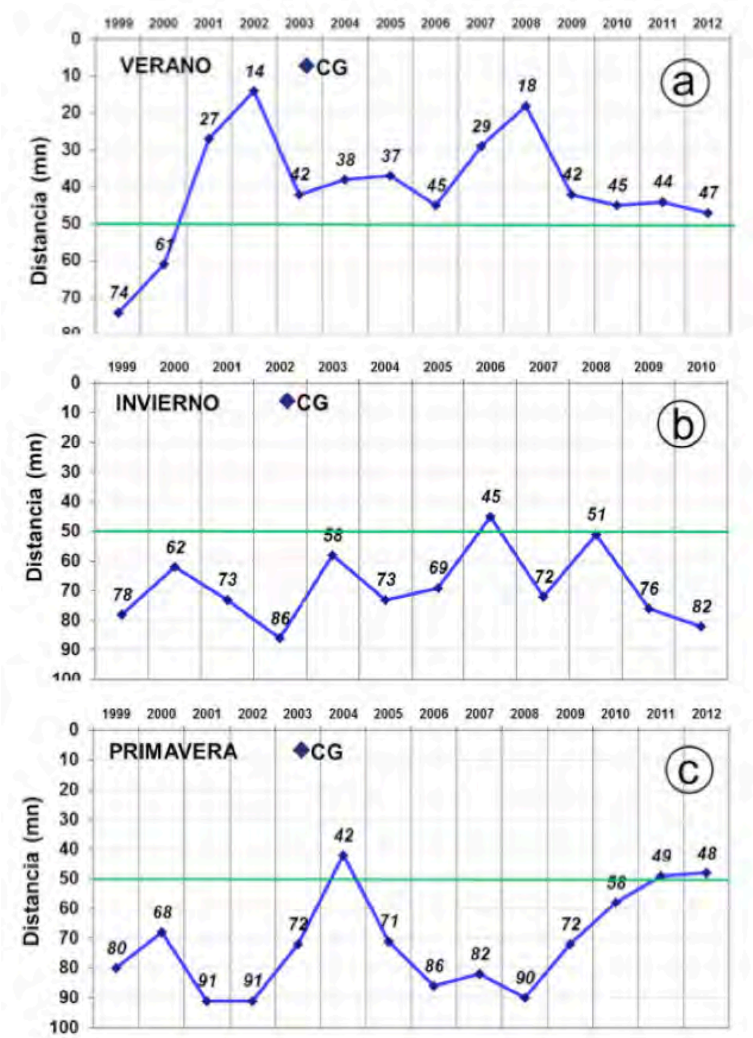

Figure 3.- Distance from the coast of the centers of gravity of the acoustic abundance indexes of jumbo squid (*D. gigas*), by year. For: (a) summer, (b) winter and (c) spring. Years 1999 to 2012.

Records from the industrial and the local artisanal fishery confirm most of the above observations. In fact, the industrial jigger fleet that operated in Peruvian waters from 1991 to 2011 reported catches of jumbo squid along the whole Peruvian coast and as far as 450 nm from the cost, but most of their catches were in the northern and central part within 80 nm in summer and 100-130 nm in winter and spring. While most of the catches of the local artisanal fishery have been made within the 40 nm from the coast, mostly in the north and in the south.

3. Habitat

Adult jumbo squid has a high tolerance to changes in water pressure, temperature, salinity, dissolved oxygen and other environmental factors, which allows it to inhabit and migrate through depths from 0 to 1200 m in tropical and temperate neritic, epipelagic and mesopelagic habitats in the eastern Pacific (Anderson and Rodhouse, 2001; Nigmatullin et al., 2001; Tafur *et al*., 2001; Gilly *et al*. 2006). Is capable of extensive vertical and horizontal migrations and has a complex reproduction and recruitment pattern (Boyle and Boletzky, 1996). Is a nektonic species that forms large schools of individuals of similar size, is widely distributed over the continental slope and in the adjacent coastal and oceanic waters in the eastern Pacific and their largest concentrations are usually found in areas where primary productivity is high but not maximum, and where the zooplankton biomass is relatively high and the number of mesopelagic and bathypelagic fishes is maximum (Nesis, 1970, 1983).

Is a very aggressive predator and prey availability is a more important factor than temperature or other environmental parameters in shaping the geographic distribution of jumbo squid. Younger and/or smaller jumbo squids with mantle length (ML) up to 30 cm predominate in oceanic waters, while larger jumbo squids are more neritic (Nesis, 1970; IMARPE and Fisheries Agency of Japan, 2013).

Being a eurythermal species inhabits water masses with surface temperatures ranging from 15 to 28°C (Nesis, 1983) and even as high as 32°C in equatorial waters (Nigmatullin et al., 2001). However, in the southern hemisphere the largest concentrations are usually found in areas with surface water temperatures between 17 and 23°C, with a maximums between 18 and 20°C.

Off Peru jumbo squid has been captured at sea surface temperatures ranging from 17.5 to 27.5°C (Benites, 1985; Benites and Valdivieso, 1986; Segura et al., 1996; Yamashiro et al., 1997) and the best concentrations are usually reported throughout the range of temperatures typical of the front between the warm Surface Oceanic Waters (20.0°C) and the Cold Coastal Waters (17.8–19.6°C), with maximums where the sea surface temperature is above 18°C and is 14°C or slightly higher at 50 m depth (Rubio and Salazar, 1992; Yamashiro et al., 1997). Also, for a similar nearby area off Peru and Ecuador, Kuroiwa (1998) reports a drop in jumbo squid CPUE abundance indexes when sea surface temperatures are above 23°C while he found no correlation between CPUE and sea surface temperature at ranges between 16° and 23°C. He also found that in this area jumbo squid catches were higher when the thermocline was at 10 to 50 m depth with temperatures of 15.0° to 15.9°C, and catches were poorer when warm-water masses reach depths of 30-40 m or when cold-water masses prevail on the surface.

In general, it has been observed that the highest concentrations of jumbo squid are found along the external border of the main upwelling areas in association with the continental slope and the front of confluence between the warm Surface Oceanic Waters and the Cold Coastal Waters, where mesopelagic fishes and other potential preys are abundant enough to support jumbo squid high growth rates.

It has been observed that off Peru there are groups of jumbo squids that reach sexual maturity at different sizes (Arguelles et al, 2008) and ages (Arkhipkin et al, 2015). This seems to be somehow related to the high intra- and inter-annual variability in the oceanographic conditions typical of the Peruvian Humboldt Current System, which in turn could determine changes in the availability of food for juveniles and other early life history stages. On this Nesis (1983) and Nigmatullin et al (2001) proposed that there might be at least three strains, groups or population subunits of jumbo squid according to the size at which they reach sexual maturity. With one group that reaches sexual maturity latter and at larger size inhabiting colder more coastal upwelling waters; while those that mature at intermediate or smaller size inhabit slightly warmer waters farther from the coast. It has also been suggested that by remaining and spawning closer inshore, the larvae of those maturing at larger size could be more easily retained in the eddies of the eastern part of the Peruvian Humboldt Current System, favoring some degree of geographic and genetic isolation of this group.

4. Migration

Jumbo squid is known to undertake ample vertical and horizontal migrations associated with their feeding and reproduction habits. Vertical migrations can span from the surface to more than 600 m deep in a diel cycle, while longer-term inshore-offshore and latitudinal migrations of several hundred miles and horizontal movements of nearly 100 km in 3 days have been reported for this species in the eastern Pacific (Nesis, 1983; Nigmatullin et al., 2001; Gilly et al, 2006). In the Peruvian Humboldt Current System jumbo squid remains at depths of 250 to 600 m and more during the day, and migrates to surface waters during the night, moving through a wide gradient of water temperatures, salinities and dissolved oxygen while feeding on a variety of mesopelagic species that also migrate and concentrate closer to the surface at night.

The extent of the vertical distribution and dial migration of jumbo squid off Peru is illustrated by the acoustic and hydrographic profile made with the R/V José Olaya off Punta Sal (04°00'S) during winter 2000 (Figure 4), where acoustic readings, water temperature and salinity were continuously recorded from 15 to 90 nm from the coast (the maximum distance from the coast surveyed in this profile) and from the surface to 700 m deep. Significant echo traces of jumbo squid were recorded from 20 to 650 m deep at water temperatures ranging from 7° to 21°C and salinities ranging from 34.2 to 35.1 ups). As noted in Figure 4, the jumbo squid concentrations were found between 550 and 650 m during daylight (in afternoon hours and at 70-90 nm from the coast), in water masses with temperatures of 7°C and salinities of 34.20 to 34.45 ups. Then, at or around sunset (between 18:00 and 20:00 hours and at 60-75 nm from the coast) the jumbo squid concentrations were fund in intermediate depths and moving up the water column from 600 m to 120 m, and from 7°C to 14.5°C and 34.2 ups to 34.8 ups. While during the night hours (19:00 to 03:00 hours at 15-65 nm from the coast) the concentrations of jumbo squid were found above the 120 m depth in water masses with temperatures between 15°C and 21°C and salinities between 34.8 and 35.1 ups.

The horizontal migrations of jumbo squid can be passive, as when eggs, paralarvae and juveniles, and sometimes adults are transported by sea currents, or active in adults (Nigmatullin *et al*., 2001). In the Peruvian Humboldt Current System the massive horizontal feeding migrations usually take place during summer and fall, while the reproduction migrations usually occur in late winter and spring, with mature jumbo squids forming large and dense aggregations that move at speeds of 5 to 25 km/h. However, it has been noted that the extent of these horizontal migrations can be highly variable amongst individuals of the same cohort, which illustrates the high plasticity of the species to adapt to changing environmental conditions (Lorrain *et al*., 2011). Also, while being described as a migratory species jumbo squid has been found to behave as a resident species remaining for several

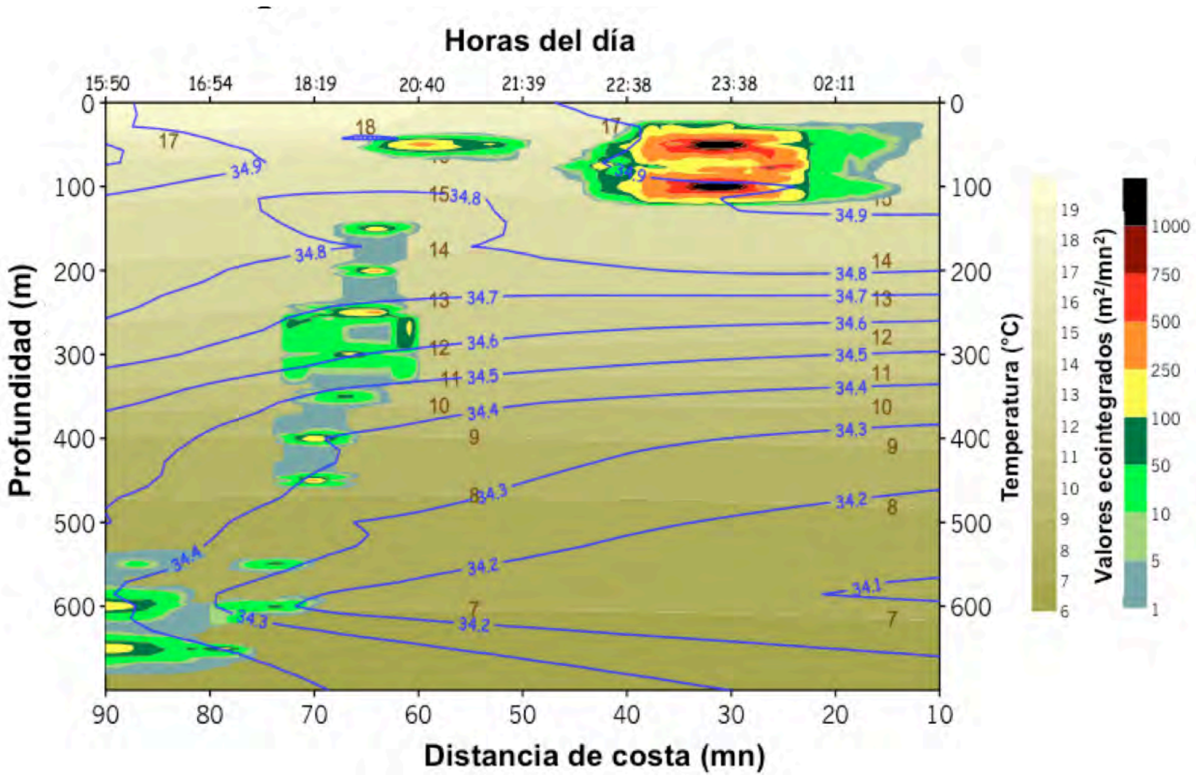

Figure 4.- Acoustic and hydrographic profile off Punta Sal (04°00'S) showing the vertical distribution and abundance of jumbo squid (*D. gigas*) in relation to the isotherms and isohalines from 10 to 90 nm from the coast, 0 to 700 m depth and time of day from 15:50 to 03:30 hours, during winter 2000 with the R/V Jose Olaya.

weeks in some feeding areas (Arguelles *et al*. 2012), probably while prey supply remains high.

The analysis of carbon isotopes in the anterior dorsal margin of the mantle shows that jumbo squid in the Peruvian Humboldt Current System performs wide longitudinal (inshore-offshore) migrations with early juveniles in oceanic waters at 200 to 400 nm from the coast, older juveniles closer inshore and maturing jumbo squids moving back offshore towards the outer edge of the continental slope and slope (Arguelles *et al*., 2012). The conceptual model in Figure 5 illustrates the offshore-inshore migration pattern of jumbo squid along its ontogenetic cycle and its relation with the distribution of preys and some key environmental parameters in the Peruvian Humboldt Current System.

5. Reproduction

Mature and spawning of jumbo squid occur along the whole Peruvian coast. Prior to 2001 larger groups of mature and spawning squids were found from the border of the continental shelf (20 to 80 nm from the coast) to as far as 200 nm both in the north, between 03° and 08°S, and in the south, between 12° and 17°S (Tafur *et al*., 2001) while paralarvae followed a similar but wider distribution pattern as that of mature and spawning squids, with large concentrations of paralarvae having been reported around 200

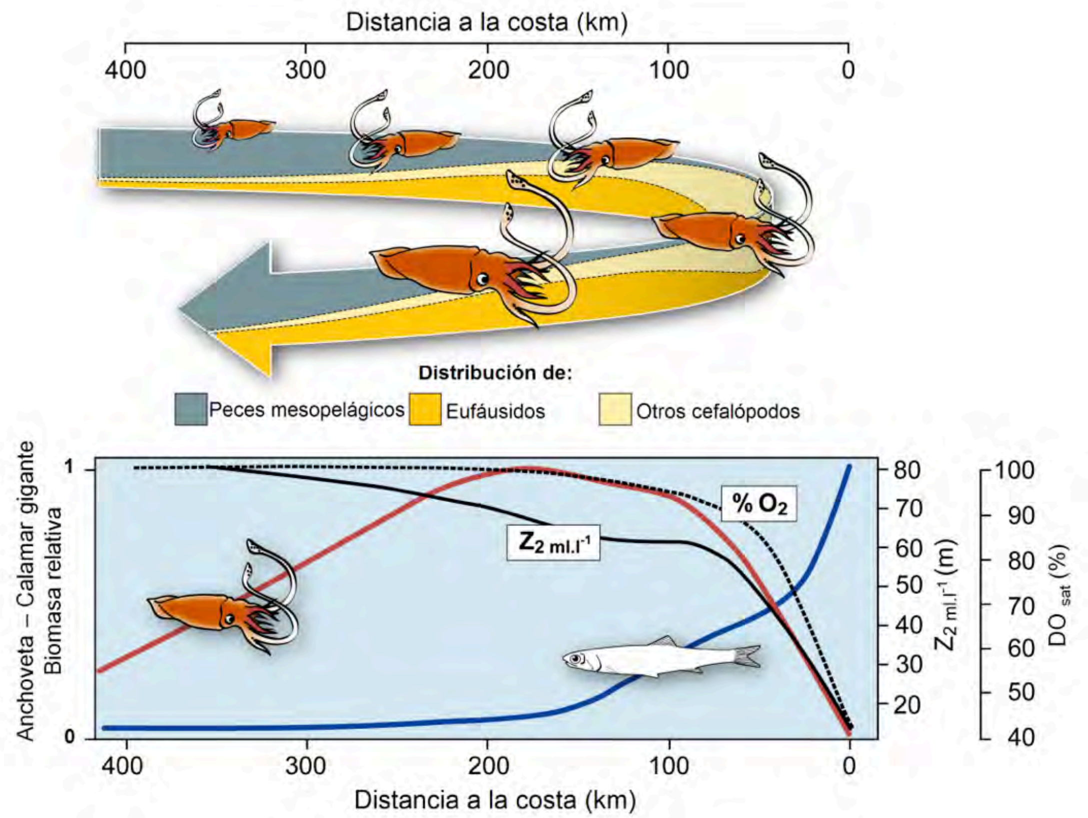

Figure 5.- Conceptual model of the inshore-offshore distribution of: (upper panel) jumbo squid (*D. gigas*) along its ontogenetic cycle in relation to the distribution and proportional abundance of its main prey groups, i.e., mesopelagic fishes, euphausids and other cephalopods; and, (lower panel) relative acoustic biomass estimates of jumbo squid (solid red line) and Peruvian anchoveta (*Engraulis ringens*) (solid blue line), and % saturation of dissolved oxygen (dotted line) and depth of the 2ml.l^{-1} isoline in m (black solid line) (from Alegre *et al*., 2014).

nm from the coast in the north (06°S) and in the south (14° to 16°S), and at about 100 nm in the center (12° to 16°S). However, more recent studies show a wider distribution of mature and spawning jumbo squid as well as paralarvae along the whole Peruvian coast from 20 to 300 nm from the coast (IMARPE, 2007; IMARPE/Fisheries Agency of Japan, 2013).

The various reproductive indices of jumbo squid being monitored by IMARPE include the gonadosomatic index (IGS) and the nidamental gland index (IGN) in females, the spermatophore complex index (SCI) in males and the index of reproductive activity in males and females (Figures 6 and 7). All these indices indicate that off Peru jumbo squid maintains some reproductive activity all year round, with an annual period of increased reproductive activity that extends from July to February the following year and peaks between October and January (spring to early summer) (Nesis, 1970, 1983; Tafur, *et al*., 1997, 2001, 2010, 2015; Yatsu *et al*., 1999).

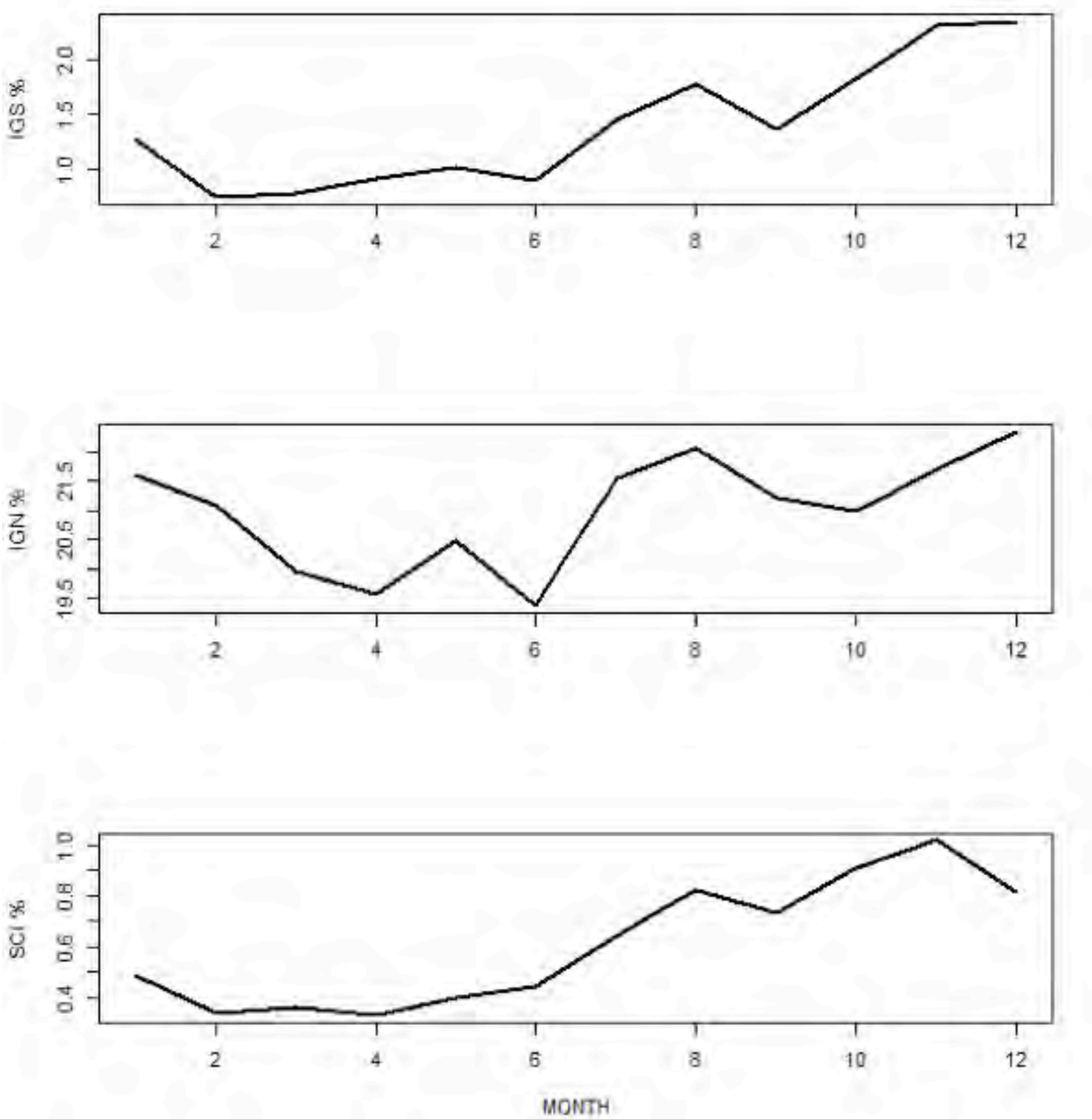

Figure 6.- Mean monthly variability of the gonadosomatic index (IGS) and the nidamental gland index (IGN) in females and the spermatophore complex index (SCI) in males of jumbo squid (*D. gigas*) in Peruvian jurisdictional waters, years 1989-2011.

Furthermore, the monthly indices of reproductive activity or proportion of females in stages III (mature) and IV (spawning) and males in stage III (mature or in evacuation) during 1989-2011 show clear differences by sex in the extent and timing of their reproductive activity. Adult males usually remain active (mature or in evacuation) in high proportions throughout the year (Figure 7, gray line), while females also remain active (mature or spawning) all year round (Figure 7, black line) but in much lower proportions and with the higher values concentrated in fewer months, usually in spring (October-December).

The highest values of reproductive activity of females occurred in spring 1997 with unusually high values protracting well into summer-early fall 1998. Particularly high levels of female reproductive activity are also observed during spring 2010 and spring 2011, while lower values are observed in 2004-2008. It is noted that the period of highest female reproductive activity observed during spring 1997 and summer-early fall 1998 occurred during the full development phase of the very strong El Niño 1997-98, while colder than normal conditions prevailed during the other periods of high female reproductive activity in spring 2010 and spring 2011 (Tafur *et al*., in press).

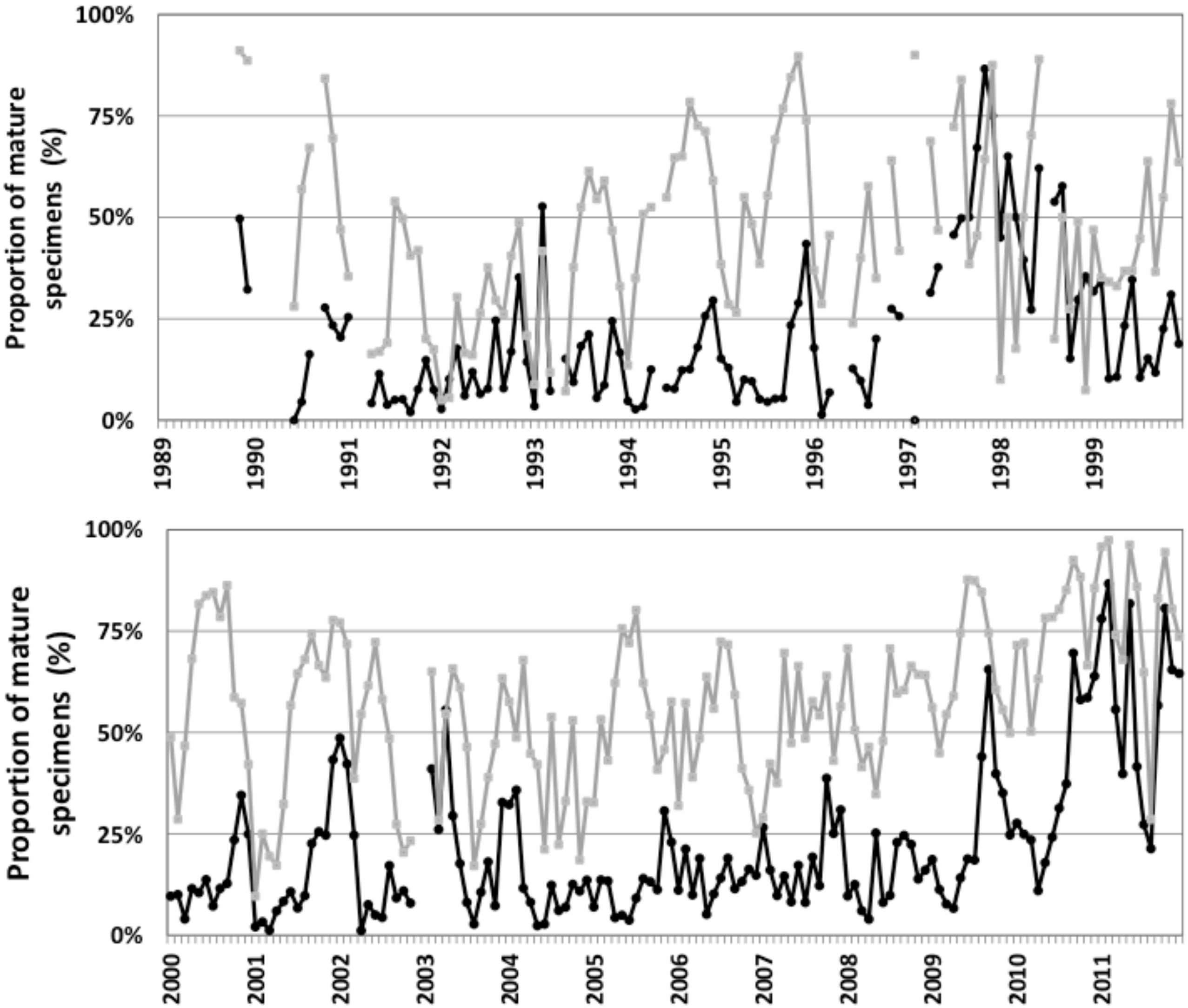

Figure 7.- Monthly variability in the proportion of mature and spawning or evacuating jumbo squid (*D. gigas*) captured in Peruvian jurisdictional waters during 1989 to 2011 (black lines = females; grey lines = males).

6. Age and growth

Early length frequency analysis of jumbo squid in Peruvian waters by Nesis (1970) estimated that a one year old jumbo squid would reach a mantle length (ML) of 20 to 35 cm, and 30 to 50 cm when 2 years old; with growth rates of 2.0 to 2.5 cm per month during the first year and 1.0 to 1.2 cm per month during the second year. He also suggested that jumbo squids larger than 50 cm ML could have 4 or more years of age. Also using length frequency analysis Arguelles (1996) identified at least two cohorts per year in jumbo squid caught in Peruvian waters between 1991 and 1994, estimating that their mantle length was between 41 and 53 cm when one year old and between 64 and 80 cm when 2 years old, with growth rates 3.9 cm per month during the first year and 2.1 cm per month during the second year of life.

Arkhipkin and Murzov (1986) were amongst the first ones to study the age and growth of jumbo squid in the southeast Pacific using hard structures. They analyzed the statoliths of 113 jumbo squids with mantle lengths between 0.9 and 49 cm collected in the Southeast Pacific between 1981 and 1984 and identified two distinct groups, differing in the size at which they reached sexual maturity. According to Arkhipkin and Murzov (1986), jumbo squid that mature at larger sizes (46-49 cm ML for females and 38-42 cm ML for males) would be 36-37 weeks old if females and 29-30 weeks old if males. While females maturing at smaller sizes (26-28 cm ML) would be younger, only 29-30 weeks old.

Then Masuda *et al*. (1998) analyzed the statoliths of 584 jumbo squids captured in the Southeast Pacific between 1987 and 1995 and reported maximum ages of 352 days for a 77 cm ML male and 378 days for an 86 cm ML female. They also estimated that the average daily growth rates varied between 1.92 and 1.54 cm for females and between 1.55 and 1.70 cm for males.

Arguelles *et al*. (2001) studied the age and growth of 134 jumbo squids captured in Peruvian waters during 1992. They estimated that the age of a 412 mm ML male was 220 days while the age of another 855 ML male was 354 days, and also estimated that the age of a 474 mm ML female was 205 days while the age of another 965 ML female was 354 days. They also report that the relative instantaneous daily growth rates of mature jumbo squids ranged from 0.08 for large mature jumbo squids and 0.58 smaller ones.

Keyl *et al* (2010) used modal progression analysis to study the growth rates, longevity, maximum size, and number of annual cohorts of jumbo squid captured in Peruvian waters between 1991 and 2007. They managed to identify a total 33 cohorts for the whole 17-year period, with a number of cohorts per year that fluctuated between 0 and 6. Their estimated growth rates also varied inter-annually, between 11 and 44 mm per month; as did the longevities, varying between 11.1 and 32.1 months; and the maximum mantle lengths, that varied between 1024 and 273 mm. They also noted that fast-growing cohorts with medium longevity and large terminal size were found during moderately cool periods; while longer-lived, slow-growing cohorts with small terminal size were found during extremely warm or extremely cold environmental periods typical of El Niño or La Niña.

These differences in growth rate, longevity and maximum size reflect the great adaptability of jumbo squid to varying environmental conditions and its capability to adjust its growth to react to these changes and to their impacts on prey supply. It is also suggested that the observed variability in growth rate, size at maturity, longevity and maximum size could be both genotypic and phenotypic.

Liu *et al* (2013) studied 1244 jumbo squids captured off the Peruvian jurisdictional waters between 10° and 18° S during 2008-2010. They estimated ages ranging from the 144 to 633 days, which confirm observations by other authors that jumbo squid is a short-lived species that could live up to almost two years. The older 633 days old jumbo squid was a female measuring 1,033 mm ML and weighting 54,500 g. The oldest male was 574 days old, measured 1,033 mm ML and weighted 33,500 g. However, the dominant groups of females and males representing almost 80% of the total were between 181 and 300 days old.

More recently Arkhipkin *et al* (2014) analyzed the inter-annual variability in the lifespan of mature jumbo squid in Peruvian waters during 1991-2011 by statoliths age readings. They found that the sea temperature during the early life history stages has a strong negative effect on the maximum age of jumbo squid and concluded that sea temperature parameters along with other environmental factors are important in determining whether a given animal would have a 1-year life cycle with early maturation and small size, or a 1.5- to 2-year life cycle with delayed maturation and large size.

7. Trophic ecology

Jumbo squid plays an important role in the Peruvian marine ecosystem both as predator and as prey. As a prey represents an important component in the diet of sperm whales in the Southeast Pacific (Vinatea, 1965; Clarke *et al*., 1998), similar to the role it plays in the Northeast Pacific (Ruiz-Cooley, 2004). As predator, jumbo squid has a wide food spectrum (Shchetinnikov, 1989; Nigmatullin *et al*., 2001) that includes invertebrate macrozooplankton, fishes and squids, with a predominance of macrozooplankton and juvenile fishes in the diet of juvenile jumbo squid and predominance of fish and cephalopods in adult jumbo squids.

IMARPE studies carried out between 2004 and 2011 (Alegre *et al*, in press) confirm that jumbo squid in the Peruvian Humboldt Current System consumes high percentages by weight of mesopelagic fishes, such as *Lampanyctus spp., Myctophum nitidulum, M. aurolaternatum, Diogenichthys laternatus* and *Vinciguerria lucetia*; as well as cephalopods, including its own species (cannibalism) and the squid *Abraliopsis affinis*, nautilus *Argonauta spp* and several species of Loliginidae; and other invertebrates like the euphausiids and squat lobster *Pleuroncodes monodon* (Figure 8). Similar studies for the Northeast Pacific (Markaida and Sosa-Nishizaki 2003; Markaida, 2006) show similarities with the diet of jumbo squid in the Southeast Pacific, with predominance of mesopelagic fishes.

These recent studies also show that out of a total of 55 prey-items, the dominant preys in weight were cephalopods (26.4%) and mesopelagic fish *Vinciguerria lucetia* (24.4%) and Myctophidae (18.3). Prey species with commercial value such as anchoveta (*Engraulis ringens*) and hake (*Merluccius gayi*) show up in very low quantities by weight (respectively 2.1% and 0.14%) during this study. The low incidence of these commercial species are in contrast with the reports of high hake (*M. gayi*) consumption by jumbo squid in Chilean waters by Ulloa *et al*. (2006), which according to Ibanez *et al* (2008) may be the result of a methodological bias due to the type of fishing gear used in their sampling.

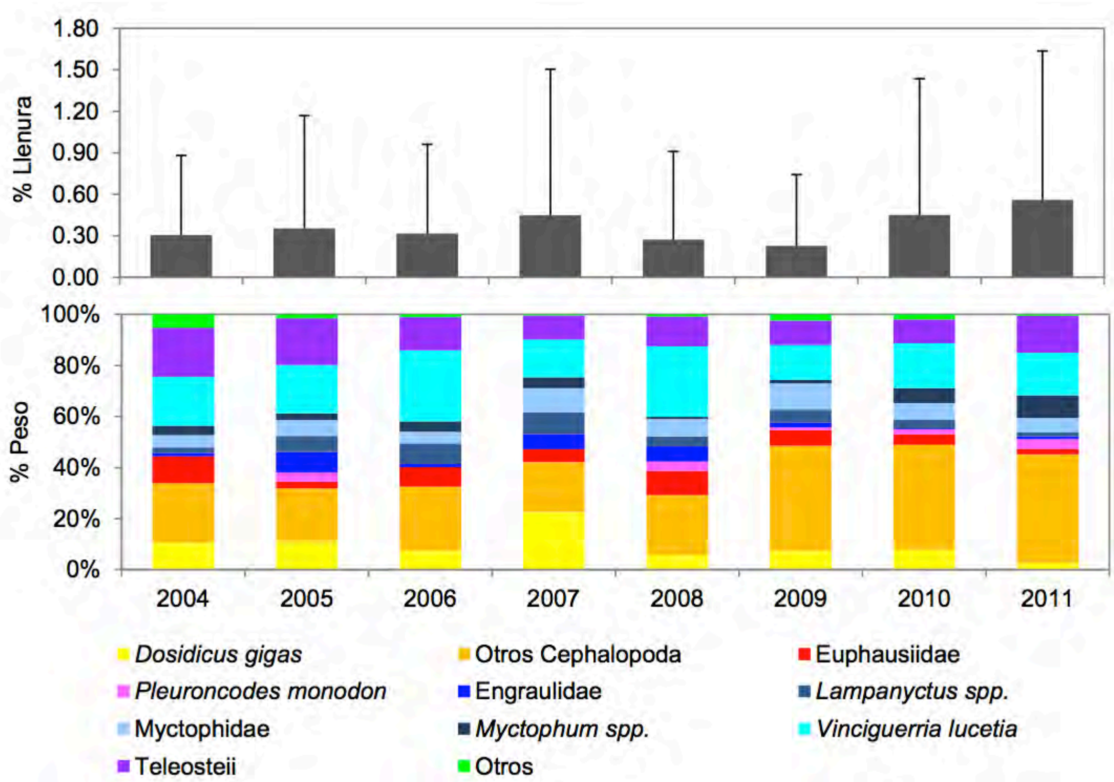

Figure 8.- Percentage weight (% Peso) of functional groups in the stomach contents of jumbo squid (*D. gigas*) captured in Peruvian jurisdictional waters between 2004 and 2011 (updated from Alegre *et al*, in press).

In fact, the Ulloa *et al*. (2006) study was made on jumbo squid caught during a hake directed trawl fishery, and it has been noted that in areas where these species coexist there is an abnormally high incidence of hake in stomach content of jumbo squid when samples are taken from catches made during the hake trawl fishery; as there is an abnormally high incidence of anchoveta in stomach content of jumbo squid when samples are taken from catches made during the anchoveta purse seine fishery. This due to the aggressiveness and active intake by jumbo squid of whatever else is found in higher than usual concentrations inside or around the fishing gear with which they end up being caught. The IMARPE study by Alegre *et al* (in press) was based on jumbo squid captured during the industrial jigger fishery and, therefore, to avoid the source of bias pointed out by Ibanez *et al*. (2008, 2009) when estimating cannibalism they discarded all fresh jumbo squid from the stomach contents of jumbo squids included in their analyses, on the grounds that this intake had been influenced by the capture or sampling method being used (jiggers with attracting lights).

The weight diet composition of jumbo squid was found to vary with the squid size (Figure 9A). There is a steady increase in the consumption of cephalopods as jumbo squid gets larger. Cephalopods (including jumbo squid) account for 24.3% of the diet of small jumbo squids (ML < 40 cm) and increases to 43.2% for larger squids (ML > 80 cm). The percentage of Euphausiidae also increases significantly with jumbo squid size, although it is also high in smallest squids. Consumption of Euphausiiidae is 6% in smaller (ML <40 cm) jumbo squids, drops to 3.5% in slightly larger (between 40 and 60 cm ML) jumbo squids, increases to 8.4% in jumbo squids between 60 and 80 cm ML and reaches 12.4% in jumbo

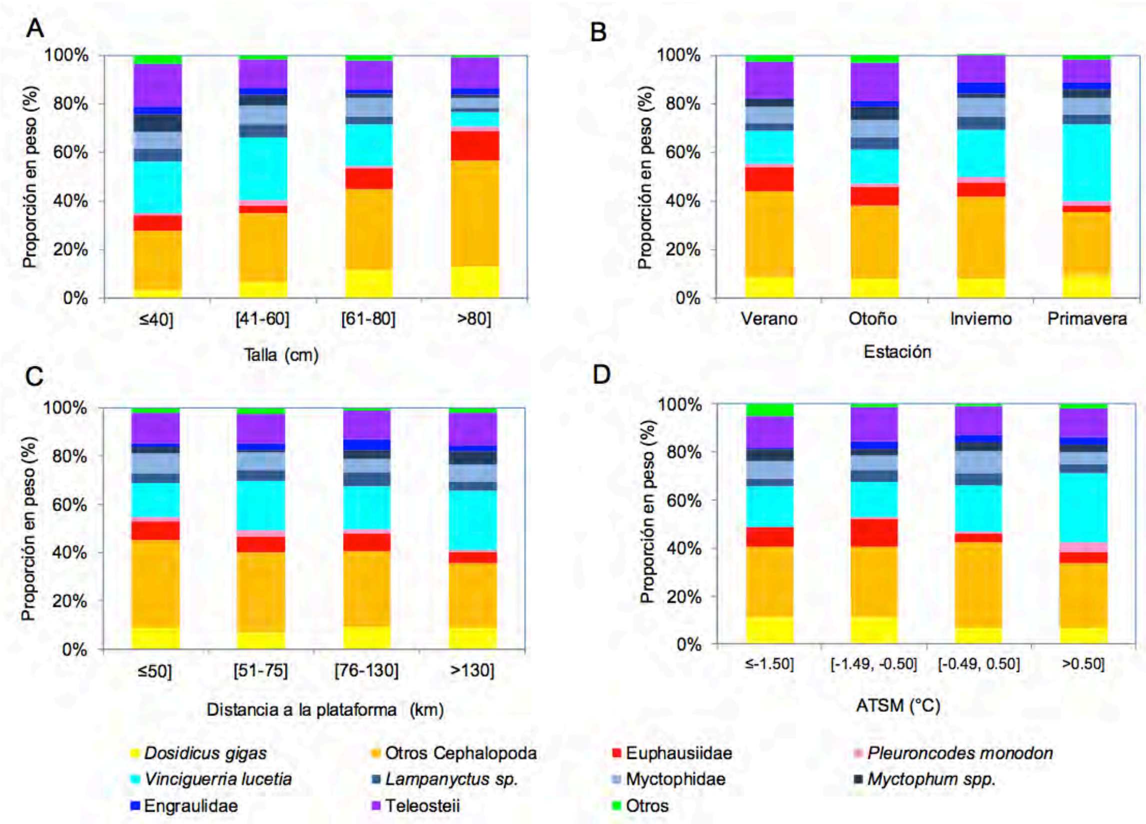

Figure 9.- Diet composition in weight (%) of jumbo squid (*D. gigas*) capture in Peruvian jurisdictional waters, by: (A) mantle size; (B) season; (C) distance from the border of the continental slope; and, (D) sea surface temperature anomalies (SSTA). Years 2004-2011 (Alegre *et al,* 2014).

squids larger than 80 cm ML. On the other hand, with the increase in mantle size there is a significant decrease in the consumption of *V. lucetia* (from 21.0% to 5.6%) and of *Myctophum spp*. (from 7.2% to 1.3%), while cannibalism increases.

There is no particular seasonal trend in the diet composition of jumbo squid (Figure 9B). However, in spring there is a significant increase (to 32%) in the percentage of *V. lucetia* and a decrease in the percentage of other Cephalopoda (to 26%), Euphausiidae (to 2.8%) and Teleosteii (to 9.3%). While in summer, Euphausiidae is at its maximum (10%), *V. lucetia* is at it's lowest (13.7%) and anchoveta (*E. ringens*) is rare (0.4%).

The diet composition of jumbo squid was found to vary significantly with the distance from the border of the continental shelf (Figure 9C). While there was only a slight decline in the consumption of Euphausiidae with the distance from the edge of the continental shelf, the percentage of other Cephalopoda decreased noticeably, from 36.3% within 50 km to 26.8% beyond 130 km, whereas *V. lucetia* increased from 13.8% within 50 km to 24.2% beyond 130 km.

Diet composition also varied with the sea surface temperature (SST) anomalies (Figure 9D). Percentage consumption of *V. lucetia* was lowest (15%) at intermediate negative SST anomalies (-1.49 to -0.50°C), increased slightly both at larger negative SST anomalies

(≤1.50°C) and at lower negative and positive SST anomalies (-0.49 to 0.50°C), while it was highest (28.6%) at positive SST anomalies above 0.50°C. There is also a significant decrease in cannibalism (from 11.0% to 6.6%) as SST anomaly values increase.

As already noted, cephalopods (including its own species through cannibalism) were found to be the main component in the diet of jumbo squid off Peru, followed by the mesopelagic fishes *V. lucetia* and *Myctophum spp.* which coexist with jumbo squid and are found to be in great abundance with estimated biomasses exceeding 10 million tons in Peruvian jurisdictional waters (Castle and Aliaga, 2000; Rosas *et al*, 2011).

The general distribution and ontogenetic trophic migration of jumbo squid is summarized in the simplified conceptual model in Figure 5 above, showing that small jumbo squids (<400 mm) are mostly found far from the coast, beyond the continental slope, where they mainly feed on mesopelagic fishes like *V. lucetia* and *Myctophum spp*. As they grow they move closer to the coast and increase their consumption of cephalopods. Then, larger squids move off the coast, towards the edge of the continental shelf but without reaching the oceanic distribution of smaller jumbo squids, where they increase their consumption of cephalopods (including cannibalism) and euphausiids (Lorrain *et al*., 2011; Argüelles *et al*., 2012; Alegre *et al*., 2014).

In principle, given its shape and small size, euphausiids may not appear as an attractive prey for an aggressive predator like jumbo squid. However, the intake of this small prey increases significantly once jumbo squids are over the continental slope, most likely due to their great abundance, easy availability and high energetic food value.

As outlined in the conceptual model in Figure 5, jumbo squid doesn't occupy the coastal waters where most of the high biomass of anchoveta (*E. ringens*) is found, and this explains the low consumption of anchoveta by jumbo squid. Contrary to what occurs off California (Field *et al*., 2013), off Peru jumbo squid doesn't enter into coastal waters where oxygen saturation is very low since, even if jumbo squid can live in deep hypoxic waters during the day, at night needs normoxic waters to recover (Seibel, 2013). This limits the co-occurrence and the predator-prey interaction of these two species to those occasions in which there is an intrusion of oceanic waters towards the coast.

8. Population units

Some authors propose only two stock units of jumbo squid over its entire range, one in the northern hemisphere and the other in the southern hemisphere (Wormuth, 1976, 1998; Nesis, 1983; Clarke and Paliza, 2000).

However, Nigmatullin *et al* (2001) recognize the difficulties to define the population structure of jumbo squid but note that there might be some allopatric groups (separated by physical barriers) and that there are many sympatric and parapatric groups which differ from each other in many important ecological aspects. They also describe at least three intraspecific groups or population sub-units, distinguishable by the sizes at which females and males reach sexual maturity. A first group that mature at small size (130-260 mm ML for males and 140-340 mm ML for females) and is found predominantly in the near-equatorial area. A second group that mature at medium sizes (240-420 mm ML for males and 280-600 mm ML females) and is found over the whole species range except at the higher latitudes. And a third group that mature at larger sizes (400-500 mm ML and over for females and 550-650 and over for males) and can be found northward of 10-15°N as well as southward of 10-15°S). These three groups seem to be present in the Peruvian Humboldt Current System, off Peru.

Genetic studies have confirmed that jumbo squid off Mexico (NE Pacific) and off Peru (SE Pacific) belong to separate populations (Sandoval *et al*., 2007, 2010; Staff *et al*., 2010). No relevant genetic differences have been found between jumbo squid in Chile and Peru (Ibanez, 2010; Ibáñez *et al*., 2011) and genetic studies by Sandoval *et al* (2009) found no relevant genetic differences amongst the three size-groups proposed by Nigmatullin *et al* (2001). However, the absence of clearly defined genetic markers doesn't exclude the possibility of the SE Pacific jumbo squid population being form by multiple self sustained stock units with little genetic differentiation but distinct and to some degree independent reproductive and somatic growth processes.

Also, as noted above, jumbo squid off Peru is known to perform regular longitudinal (inshore-offshore) ontogenetic migrations over at least 200-300 nm in their life cycle, while there are no indications of noticeable latitudinal displacements associated with these ontogenetic migrations. However, there are some indications of ample latitudinal migrations of jumbo squid associated with the advance of abnormally warm or abnormally cold environmental conditions in some years.

Moreover, as also noted above, at least three groups of jumbo squid reaching sexual maturity at different sizes (Arguelles *et al*, 2008; Arguelles and Tafur, 2010) or ages (Arkipkhim *et al*., 2014) and with slightly different environmental preferences have been observed off Peru. It is highly likely that these may correspond to the three strains, groups or population subunits of jumbo squid proposed by Nesis (1983) and Nigmatullin *et al* (2001).

9. Historical catches

There are two clear periods in the development of the jumbo squid fishery in Peru. The first one between 1990 and 1996 corresponds to the initial growth of a directed local artisanal fishery and the initial development of an industrial squid fishery using foreign industrial jigger vessels under license arrangements. Together these fisheries yield a total catch of 210,000 t in 1994 and confirmed the presence of dense concentrations of jumbo squid of

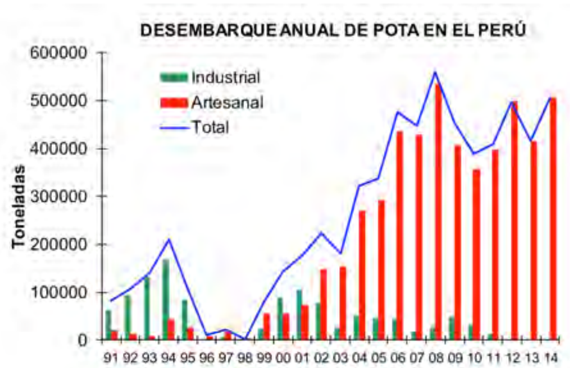

Figure 10.- Annual catches of jumbo squid (*D. gigas*) in Peruvian jurisdictional waters by the industrial and the artisanal fleet, years 1991-2014.

commercial importance in Peruvian waters (Figure 10). The second period from 1999 to-date corresponds to a phase of rapid development of the local artisanal fishery and a gradual phasing out of the foreign industrial fishery. Total catches in Peruvian jurisdictional waters in this second period peak at 559,000 t in 2008; 95.4% (533,000 t) of which were taken by the local artisanal fleet. The total in 2014 was 506,000 t, all taken by local artisanal vessels..

10. Fishing areas

Jumbo squid is caught along the whole Peruvian coast, from very close to the coast to as far as 450 nm. However, the best fishing grounds are generally found between 10 and 80 nm from the coast in summer and 10 to 130 nm in winter and spring, with the industrial fleet fishing offshore and the artisanal fleet usually operating closer inshore.

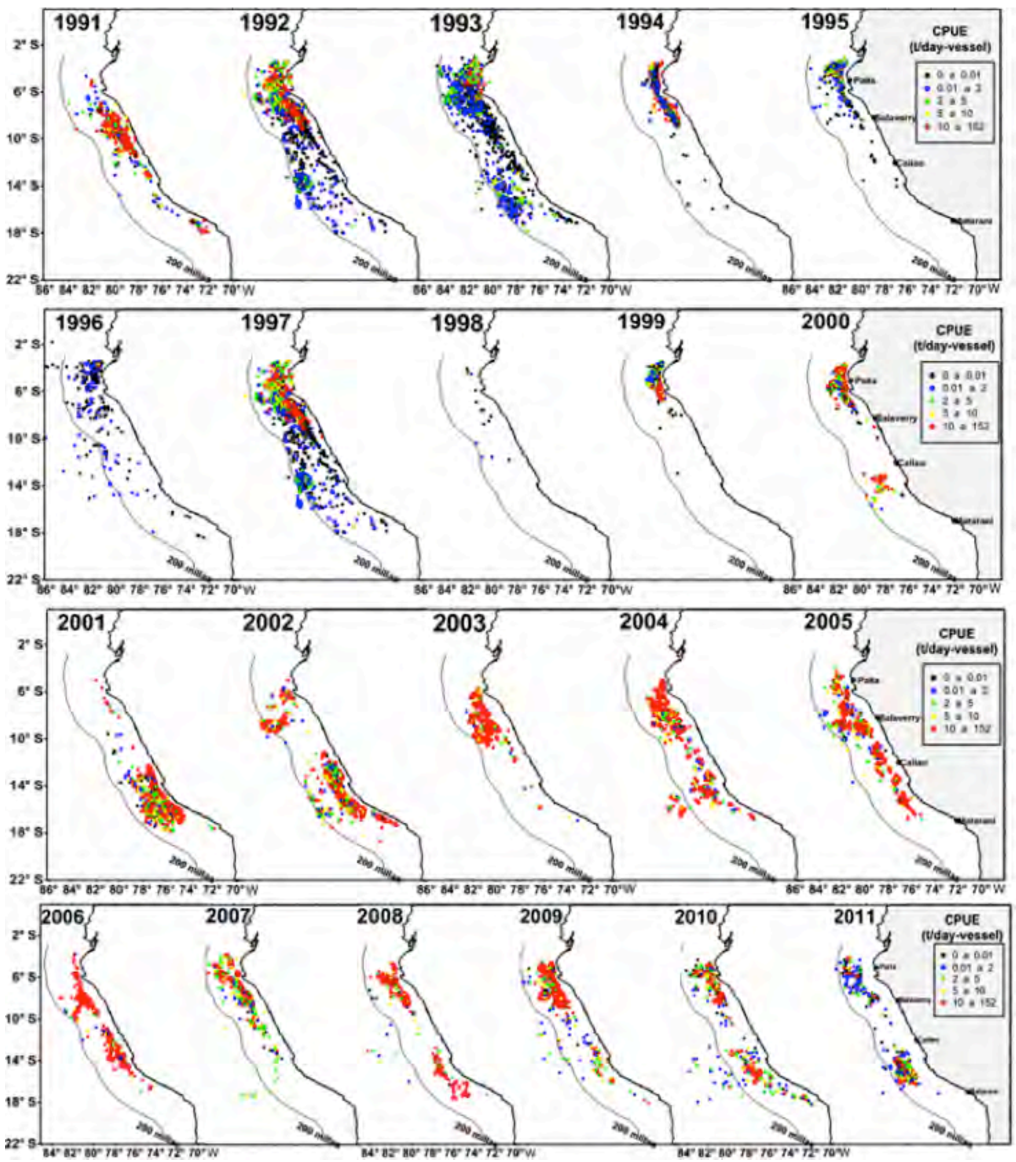

Figure 11.- Geographical distribution and abundance (CPUE, in tonnes/vessel/day) of jumbo squid (*D. gigas*) caught by the industrial jigger fleet off Peru between 1991 and 2011.

The fleet of industrial jigger vessels that operated in Peruvian waters between 1991 and 2011 captured jumbo squid along the whole Peruvian coast, beyond 20 to 30 nm from the coast until 2010 and beyond 80 nm in 2011, with catches reported as far as 450 nm from the coast. However, they found the best concentrations and made most of their catches within 200 nm from the coast, within Peruvian jurisdictional waters, over or slightly beyond the edge of the continental shelf (Figures 11 and 12).

Between 1991 and 2000 the main and most productive fishing grounds of the industrial fleet were located in northern Peru, between the 04°S and 09°S, spreading also to the central and southern part of Peru in 1992, 1993 and 1997 and then more frequently between 2001 and 2011 (Figure 11).

The best jumbo squid concentrations and the highest CPUE values (higher than 6 tonnes/vessels/hour) were found within 80 miles from the coast in summer, within 100 miles in fall and within 130 miles in winter and spring (Figure 12). Vertically, this fleet captured jumbo squid at depths from 0 to 250 m although the highest values of CPUE were obtained when jigging at depths of 20 to 150 m, with maximum CPUE rates between 40 and 60 m, particularly in summer. No licenses to fish for jumbo squid with industrial jigger

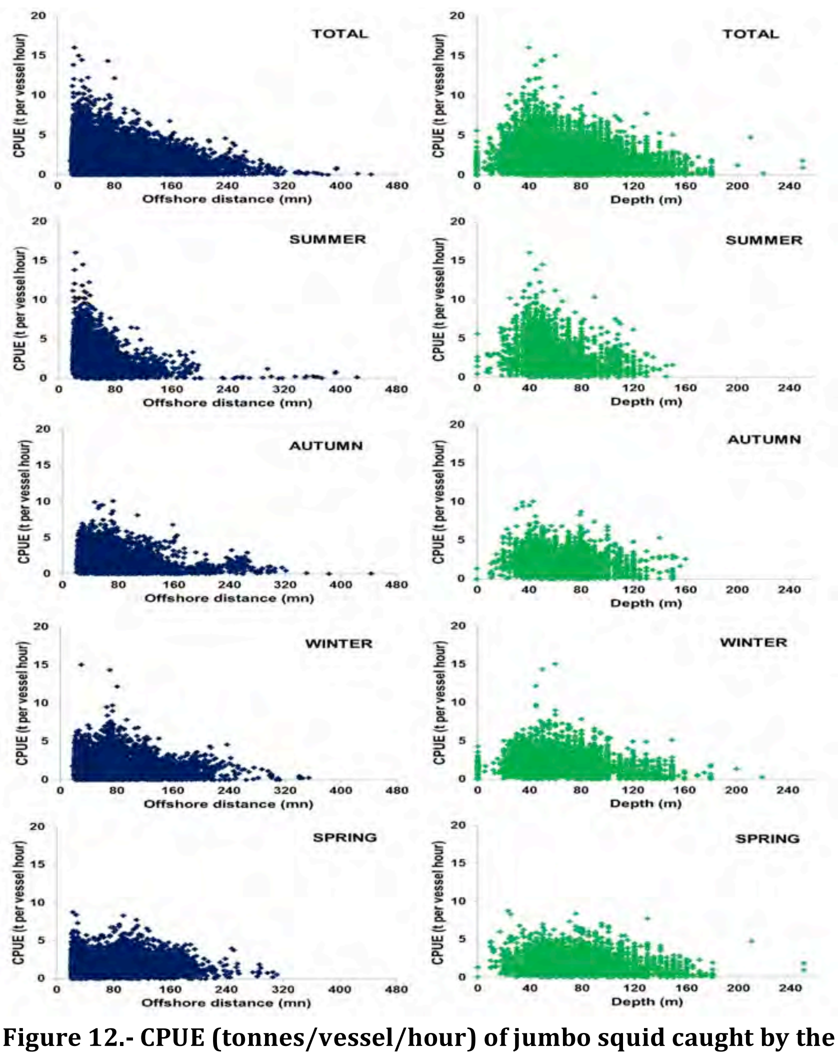

Figure 12.- CPUE (tonnes/vessel/hour) of jumbo squid caught by the industrial jigger fleet off Peru, by distance from the coast (nm) and fishing depth (m), years 1999-2001.

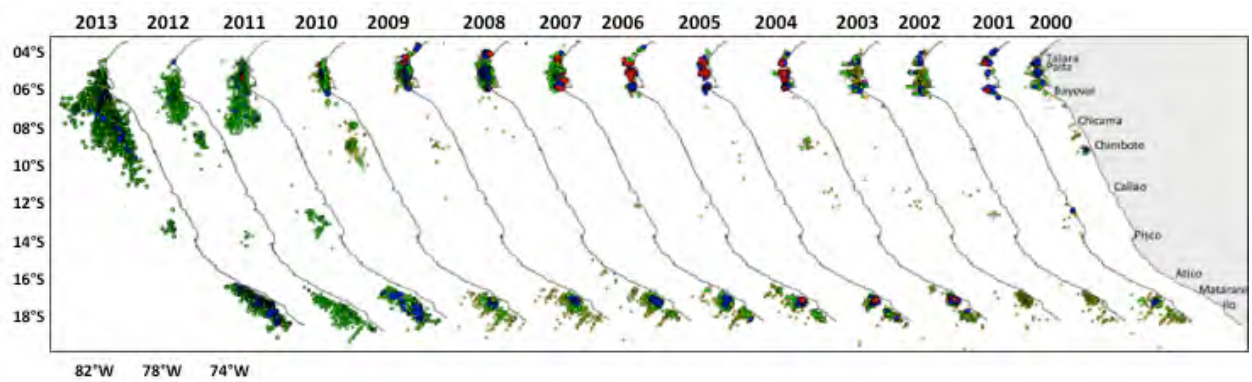

Figure 13.- Geographical distribution of jumbo squid (*D. gigas*) catches by the artisanal fleet off Peru from 2000 to 2013.

vessels in Peruvian jurisdictional waters have been granted since 2012, and since then all the catches of jumbo squid in Peruvian waters are made closer inshore by an expanding local artisanal fishery.

The artisanal fleet has little or no area restrictions to operate and since 2000 most (93.9%) of their catches of jumbo squid have been made within the 40 nm from the coast in two major areas. The main one in the north, associated to artisanal landing sites between Mancora and Bayovar (04°00' to 05°50'S) and another one in the south, with main landing sites between Matarani and Ilo (17°00' to 18°00'S) (Figure 13).

Catches of jumbo squid by the artisanal fleet are also reported outside these northern and southern main general areas and at greater distances from the coast, off Chicama (07°51'S), Chimbote (09°03'S), Callao (12°03'S) and Pucusana (12°28'S). However, these catches mainly occurred in years associated with some environmental perturbation or are made by longliners or other artisanal vessels that usually target dolphinfish (*Coryphaena hippurus*), sharks or other species and carry jiggers to capture squid for bait, but finding a good shoal of jumbo squid may eventually take it to supplement their catch.

11. Size frequency distributions

The size of jumbo squid caught in Peruvian waters both during research surveys and the commercial fishery have varied significantly between years from 1958 to 2012. The observed jumbo squid size frequency distributions ranged from 28 to 107 cm ML with mean at 72.9 cm from 1958 to 1962; from 7 to 39 cm ML with annual means between 22.9 and 25.5 cm ML in 1979-1983; from 16 to 76 cm ML with annual means between 31.8 and 34.1 cm ML in 1989-1990; from 9 to 109 cm ML with annual means between 28.3 and 44.0 cm ML in 1991-1999; and, from 13 to 133 cm ML with annual means between 49.8 and 88 ML in 2000-2012.

The size frequency distribution of jumbo squid in both the artisanal and the industrial fishery changed significantly from 2000 onwards. From 1989 to 1999 most if not all of the jumbo squid except for 1992 was under 50 cm ML, with one or two modes between 20 and 40 cm ML. While since 2000 there is a prevalence of jumbo squid larger than 50 cm ML with 2 or 3 modal sizes which could be as small as 22 cm ML (as in 2007 and 2010) or as large as 93 cm ML as in 2011 (Figure 14).

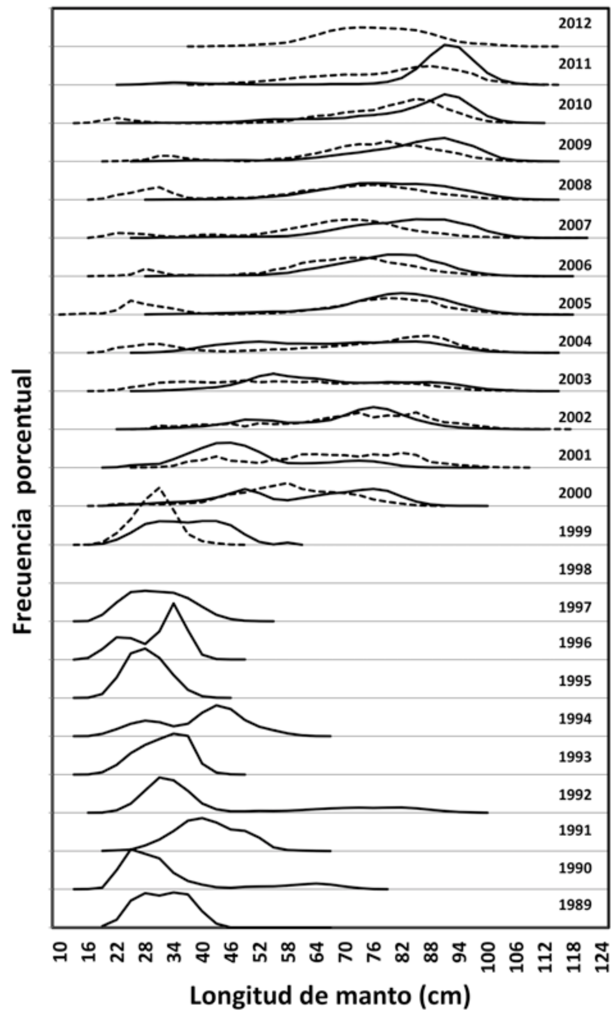

Figure 14.- length frequency distribution of jumbo squid (*D. gigas*) captured in Peruvian jurisdictional waters by the artisanal fleet (broken lines) and by the industrial jigger fleet (solid lines), by year, years 1989 to 2012.

A within year longitudinal (inshore-offshore) variability in the size frequency distribution of jumbo squid has also been observed (Arguelles *et al*., in press), which is represented by the conceptual model in Figure 5. Smaller juveniles are usually found farther offshore in oceanic waters; larger juveniles are found closer inshore, over the continental slope and into more coastal areas over the shelf; while larger (maturing) squids are found back offshore over the edge of the continental shelf and slope. No major within year differences or distinguishable trends have been noted in the latitudinal size frequency distribution of jumbo squid in the area.

While the three groups maturing at different sizes described by Nesis (1983) and Nigmatullin *et al* (2001) have also been observed in the Peruvian Humboldt Current System, these groups don't usually occur simultaneously in the jumbo squid fishery within the Peruvian jurisdictional waters. Since 2000 the only group observed in the Peruvian fishery is the one maturing al larger size, while prior to 2000 the only group observed was the one maturing at medium size, except for 1992 when both groups were observed. However, jumbo squid belonging to the group maturing at smaller size has been reported farther offshore, in the western part of the he Peruvian jurisdictional waters and in the adjacent high seas by some research surveys and by long-range jigger fleets fishing in the high seas (Liu *et al*., 2013)

12. Stock assessment

Since 1999 the assessments of jumbo squid in Peruvian waters has been based predominantly on the biomass estimates obtained through hydro-acoustic surveys conducted on a regular basis by IMARPE (Castillo and Aliaga, 2000; Castillo *et al*., 2009; Segura *et al*, 1996; Flores *et al.*, 2015; IMARPE. 2015), complemented by the monitoring of size frequency distributions and CPUE from the industrial and the artisanal fisheries to obtain an as early as possible estimate of entering recruits. More recently, as longer CPUE data-series have become available, the jumbo squid assessments have also included the application of a surplus production model (IMARPE, 2015a).

Leslie or De Lury type of stock depletion models have not been used successfully with jumbo squid in the Peruvian Humboldt Current System. Mainly due to the complexity of its reproduction, recruitment and migration patterns and the resulting multimodal size frequency distribution in the fisheries throughout the year, which makes it very difficult to identify and track throughout a the year the several cohorts or modal sizes occurring within a single year class.

Acoustic biomass estimates

IMARPE has been using acoustic surveys to assess the biomass of anchoveta (*E. ringens*) and other species since the 1960s and the estimates of these surveys were substantially improved with the introduction of the eco-integration method in the early 1970s (Johannesson and Robles, 1977). Since 1999 IMARPE modified slightly the design and coverage of its regular acoustic surveys to also include jumbo squid in addition to other important species. The surveys follow a sampling design that is systematic parallel with transects perpendicular to the coast every 12 to 17 nm (Johannesson *et al*., 1977; MacLennan and Simmonds, 1992). The equipment used has been upgraded regularly, and in recent years the acoustic data has been collected using SIMRAD scientific echo sounders model EK500 and EK60, with transducers at frequencies of 38, 120 and 200 kHz. The software “Echoview” is used for the post-processing. The hydro-acoustic equipment is calibrated at the beginning of each survey using copper spheres of 23 mm (for 120 kHz), 60 mm (for 38 kHz) and 13.7 mm (for 200 kHz) as standard targets (Foote *et al*., 1987; SIMRAD 1991, 2003) using areas of copper of 23 mm (120 kHz), 60 mm (38 kHz) and 13.7 mm (200 kHz). Also, when more than one vessel is used there is an inter-calibration to standardize the measurements of their acoustic systems.

Due to their combined priority, these acoustic surveys usually cover the whole coastal area of the Peruvian jurisdictional waters from north to south and from 10 to 100 nm distance from the coast, with some transects to only to 80 nm and others to as far as 120 nm from the coast depending on the environmental conditions and the distribution of anchoveta, the main target species in most of these surveys. It is therefore known that by only covering the coastal area from 10 to 100 nm from the coast, these surveys provide biomass estimates of only part of the jumbo squid stock and as explained in sections 2 and 4 and Figures 1, 2 and 3, the portion of the stock found within the 100 nm from the coast can vary greatly seasonally with the ontogenetic cycle as well as between years due to changing

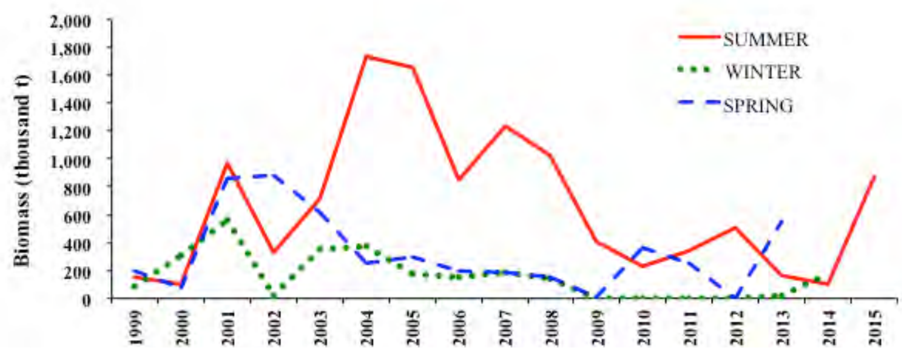

Figure 15.- Acoustic biomass estimates of jumbo squid (*D. gigas*) by season, years 1999-2015, within 100 nm from the coast along the whole Peruvian coast (years 1999-2014) and within 270 nm from the coast in selected areas to the north and and south of the Peruvian coast (summer 2015).

environmental conditions affecting the geographical distribution of jumbo squid. Therefore, these biomass estimates are to be taken as the minimum biomass of jumbo squid available in Peruvian jurisdictional waters at a given time.

An acoustic survey specifically designed to assess the biomass of jumbo squid with an extended offshore coverage was conducted by IMARPE during summer 2015 (IMARPE 2015a), but this only focused on the more northern and southern distribution of jumbo squid, covering the main fishing areas of the local artisanal fleets targeting jumbo squid with profiles going as far as 270 nm from the coast. Again, providing only a partial estimate of the biomass of jumbo squid available in Peruvian waters but presumably providing a better more focused assessment of the available biomass available to the Peruvian local artisanal fleet that as noted in Figure 5 is concentrated in the north and in the south.

The biomass estimates obtained through these acoustic surveys by season between 1999 and 2015 are shown in Figure 15. As noted, there is a high variability in the estimated total jumbo squid within the 100 nm from the coast, with the summer estimates usually being the highest and the winter estimates the lowest. The maximum estimated biomass within the 100 nm was 1.7 million t in summer 2004 and in summer 2015 the estimated biomass within 270 nm from the coast in the north (04°00’ to 08°00’S) and in the south (15°00’ to 19°00’S) was 887 thousand t.

Surplus production model

A recent attempt to assess the state of exploitation of jumbo squid in Peruvian Humboldt Current System was made by applying a biomass dynamic model with catch and effort data from the industrial and artisanal fishery in Peruvian jurisdictional waters and catch data from the long-range fleets fishing in the adjacent high seas during the period 1999-2014.

Effort and CPUE for the whole series was standardized to that of the industrial fleet in the period 1999-2011, since this fleet operated more or less uniformly along the whole Peruvian coast from 20-30 miles from the coast to as far as 200 nm, while the artisanal fleet fishing for jumbo squid operates closer to the coast and is mostly concentrated in the north and in the south (Figures 11 and 13).

Two CPUE series were used to fit the biomass dynamic model: one as catch per fishing days (t/day) and the other one as catch per fishing hours (t/hour). CPUE in t/day seems to reflect better the effect of environmental variability, whereas CPUE in t/hour appears to be better in reflecting the local squid abundance.

A Bayesian approach was used to deal with the uncertainty on which CPUE would be better in reflecting trends in total abundance. Some inferences were made about the parameters of the model by considering them as random variables with some probability distribution. The biomass dynamic model was fitted using the JAGS program for analyzing Bayesian graphical models via Markov Chain Monte Carlo (MCMC) described by Plummer (2003), assuming the following *a priori* values for the parameters of the biomass dynamic model:

$r \sim$ Normal (1.46, 1000)
$k \sim$ Log normal (13.4, 1000)
$B_o \sim$ Log normal (13.4, 1000)

The resulting population parameters estimated for the period 1999-2014 for the whole distribution area, including the Peruvian jurisdictional waters and the adjacent high seas were: the carrying capacity (K) = 4.23 million t; the rate of population growth (r) = 1.33 per year; the maximum sustainable yield (MSY) = 1.40 million t per year; and the annual fishing mortality at MSY (F_{MSY}) = 0.66. While the estimated maximum sustainable yield for only the Peruvian jurisdictional waters was estimated as (MSY') = 1.05 million t per year.
The catches estimated after fitting the biomass dynamic model with the two CPUE values (t/day and t/hour) show the same general trend as the observed catches although there are yearly differences in the simulated catches with the two different CPUE input data sets (Figure 16, top left). The CPUEs estimated by the model show an increase from 1999 to 2000 to then remain almost stable (Figure 16, bottom left). The estimated annual biomass values show a slight decreasing after a maximum mean value of 3.9 million t estimated for 2002 (Figure 16, top right). The estimated fishing mortality (F) shows some variability with a general increasing trend (Figure 16, bottom right) with a maximum value of F= 0.2 in 2014, still well below the estimated F_{MSY} reference value, indicating a situation of under-exploitation.

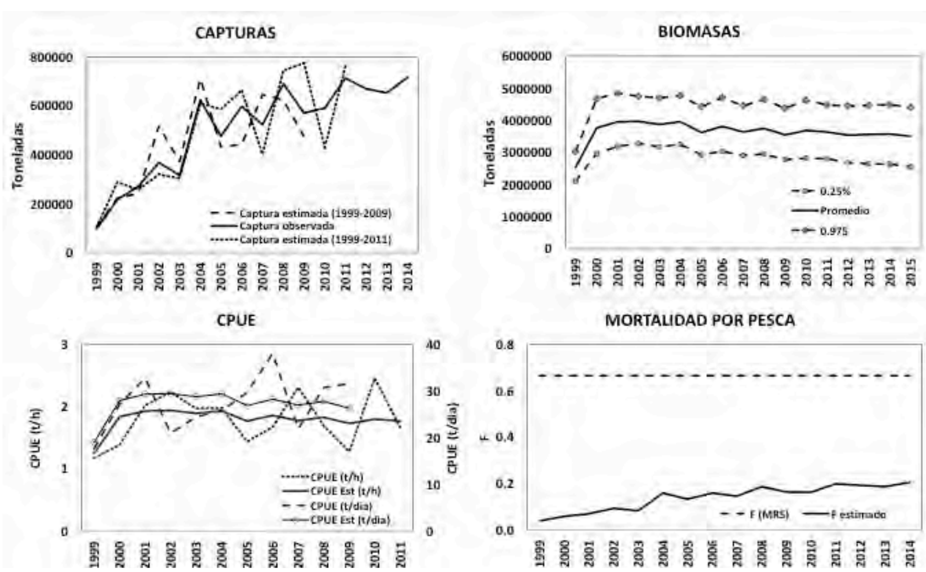

Figure 16.- Observed and estimated values of annual catch (top left), biomass (top right), CPUE (bottom left) and fishing mortality (bottom right), with the dynamic biomass model, years 1999-2014.

13. Fisheries management

The Peruvian jumbo squid fishery had its initial development during the late 1980s and early 1990s. Currently is the second most important fishery in Peru, both in terms of volume and foreign exchange income since most of the catches go to the export market. Also, this fishery has a noticeable social impact because since 2012 is carried out entirely by local artisanal fleets.

No specific management regulations regarding jumbo squid fisheries were in place in Peru prior to 1990, mainly because there was no squid directed fishery, and landings resulting mostly from incidental catches were very small. The first management measures regarding jumbo squid fisheries were adopted by Peru in 1991, when under bilateral agreements Peru granted fishing licenses to up to 31 industrial jigger vessels from Japan and Korea to fish for jumbo squid in Peruvian waters between 1991 and 1995. The granting of licenses and operations of these vessels were regulated by a series of by-laws (Supreme-Decree Nº 005-91-PE; Supreme-Decree Nº 004-92-PE and Supreme-Decree N°008-92-PE). These included fishing effort regulations, catch quotas, fishing area limitations and minimum size limits. As fisheries developed, a more formal Fisheries Management Plan for Jumbo Squid (R.M. N° 155-94-PE) was approved and entered into force in 1994 (Guevara *et al*, in press), which amongst other measures included a quota system by vessel and type of fleet, fishing area regulations, and provision to stimulate the development of a local jumbo squid artisanal fishery.

While the artisanal fleet has no fishing area regulations other than the one that prevents fishing within 200 m from islands and selected seabirds nesting sites along the coast, the industrial fleet fishing for jumbo squid was allowed to operate outside an area closure that included the first 30 nm from the coast between 1991 and 1997, the first 20 nm between 1998 and 2010 and the first 80 nm in 2011. No license for industrial fishing has been granted or renewed beyond December 2011 and since 2012 fishing for jumbo squid in Peruvian waters has been reserved for the local artisanal fleet (Guevara *et al*, in press).

14. Research

The first exploratory fishing operations and research surveys to assess the presence and abundance of jumbo squid were conducted by IMARPE in 1979 and 1980 and these found low concentrations and low abundance levels of jumbo squid, the best concentrations at 30 nm off the northern part of the Peruvian coast and squids from 7 to 39 cm ML (Benites and Valdivieso, 1986). Similar results were found during another study conducted in 1983-1984, from which is noteworthy the reports on the presence of 3 to 4 cohorts in oceanic waters with a predominance of females at a ratio of 7:1, and the absence of landings in 1983 associated to the effects of El Niño 1982-1983 (Benites, 1985).

In 1984 the Japan Marine Fishery Resources Research Center (JAMARC) made some exploratory fishing surveys in the high seas adjacent to the Peruvian jurisdictional waters and in 1989-1990, through a cooperation agreement with IMARPE, these surveys were extended to investigate the distribution and abundance of jumbo squid in Peruvian jurisdictional waters. These surveys found jumbo squid concentrations abundant enough to support the development of a large-scale fishery for jumbo squid in Peruvian waters (Kuroiwa, 1998; Rubio and Salazar, 1992) and the presence and abundance of jumbo squid was also confirmed by exploratory fishing operations conducted between 1989 and 1991 with Japanese and Korean jigger vessels and commercial fishing by a Soviet fleet using pelagic trawls (Mariátegui and Taipe, 1996).

Further research surveys were conducted between 1997 and 2012 onboard the R/V Shinko Maru 3 and the R/V Kaiyo Maru through cooperation agreements between IMARPE, JAMARC and the Fisheries Agency of Japan. These research surveys provided valuable information on the distribution and concentration of paralarvae, juveniles and adults of jumbo squid as well as on their migratory behavior and the development of their early life history stages in Peruvian jurisdictional waters and in the adjacent high seas (Fisheries Agency of Japan, 1999, 2009, 2013; Yatsu, 1999; Yatsu *et al*., 1999).

IMARPE has an active research and monitoring program focusing directly on jumbo squid and its fisheries monitoring program is being reviewed to expand IMARPE observers coverage of landing sites and start placing observers on board the artisanal fleet, focusing on the artisanal fleet fishing for jumbo squid.

On a wider regional scale there is growing interest to investigate the processes and driving mechanisms that have lead to the expansion of the distribution range and the increased presence of large concentrations of jumbo squid in the northern and southern Eastern Pacific (Nigmatullin *et al*., 2001; Field *et al*., 2007; Arancibia *et al*., 2007; Zeidberg and Robinson, 2007). Particular attention is given to the possible influence of climatic changes and the effects that the depletion by fishing of potential predators of the different life-history stages of jumbo squid may have in favoring the growth and expansion of jumbo squid. Recent studies conducted by IMARPE suggest that the behavior, distribution pattern, local and total abundance, body size and time and size or age of sexual maturity could be noticeably modified under extreme warm or cold environmental conditions typical of intense El Niño and la Niña events. Further research along these lines is therefore encouraged.

15. Needs and recommendations

Some early steps may need to be taken within the SPRFMO to start puttng in place proper research and fisheries monitoring mechanisms and precautionary management measures with regards to the jumbo squid fishery in the SPRFMO Convention area. These could include:

- Promoting research on the population structure and the presence and distribution of strains, groups or population subunits of jumbo squid and their migration routes and intermix patterns throughout the Southeast Pacific;
- Promoting research on the reproductive process and the effect of environmental factors in determining the timing and the location and extension of spawning areas;
- Start monitoring and regular reporting on jumbo squid research and fishing activities in the Convention area;
- Promoting or undertaking research to obtain early estimations of recruitment and timely assessment of escapement;
- Consider the application of precautionary measures to start regulating fishery in the Convention area well before the firsts signals of population stress appear;

- Promoting research on the effects that the depletion by fishing of potential predators of the different life-history stages of jumbo squid may have in favoring the growth and expansion of jumbo squid;
- Promoting or undertaking an investigation to determine the most suitable stock assessment models and/or methods to be used to assess the stock or stocks of jumbo squid within the context of the SPRFMO; and,
- Promoting research on the changes in growth rate and the possible effect of changing environmental conditions.

16. References

Alegre, A., F. Ménard, R. Tafur, P. Espinoza, J. Argüelles, V. Maehara, O. Flores, M. Simier & A. Bertrand. 2014. Comprehensive model of Jumbo squid *Dosidicus gigas* trophic ecology in the Northern Humboldt current system. PLoS One 9, e85919. doi:10.1371/journal.pone.0085919

Alegre, A., Tafur, R., Espinoza, P., Argüelles, J., Maehara, V., Simier, M., Ménard, F., Bertrand, A. In press. Alimentación del calamar gigante (*Dosidicus gigas*, D'Orbigny, 1835) frente al Perú. Bol. Inst. Mar. Perú (in press): xxp

Anderson, C.I.H. & P.G. Rodhouse. 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. Fisheries Research, 54: 133–143.

Arancibia, H., M. Barros, S. Neira, U. Markaida, C. Yamashiro, C. Salinas, L. Icochea, L. Cubillos, Ch. Ibáñez, R. León, M. Pedraza, E. Acuña, A.Cortés & V. Kesternich. 2007. Informe Final proyecto FIP 2005-38. Análisis del impacto de la jibia en las pesquerías chilenas de peces demersales. Universidad de Concepción / Universidad Católica del Norte, 299 pp. + anexos.

Arguelles, J., 1996. Crecimiento y reclutamiento del calamar gigante *Dosidicus gigas* en el Perú (1991-1994). Informe progresivo Instituto del Mar del Perú N°23: 14p.

Argüelles, J., P. Rodhouse, P. Villegas & G. Castillo. 2001. Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. Fisheries Research 54: 51-61.

Argüelles, J., Tafur, R., Taipe, A., Villegas, P., Keyl, F., Dominguez, N., Salazar, M., 2008. Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. Progress in Oceanography 79: 308-312

Argüelles, J. & Tafur, R., 2010. New insights on the biology of the jumbo squid *Dosidicus gigas* in the Northern Humboldt Current System: size at maturity, somatic and reproductive investment. Fisheries Research 106: 185-192.

Argüelles, J., A. Lorrain, Y. Cherel, M. Graco, R. Tafur, A. Alegre, P. Espinoza, A. Taipe, P. Ayón & A. Bertrand. 2012. Tracking habitat and resource use for the jumbo squid *Dosidicus gigas*: a stable isotope analysis in the Northern Humboldt Current System. Mar. Biol. 159: 2105–2116

Arguelles, J., Taipe, A., In press. Variabilidad espacio temporal de la estructura por tallas de *Dosidicus gigas* en aguas peruanas entre 1958 y 2012. Bol. Inst. Mar. Perú (in press): xxp

Arkhipkin, A. & S. Murzov. 1986. Age and growth patterns *of Dosidicus gigas* (Ommastrephidae). In: Ivanov, B. (Ed.), Present State of Fishery for Squids and Prospects of its Development. VNIRO Press, Moscow, 107-123 (in Russian, Spanish Translation).

Arkhipkin, A., J. Argüelles, Z. Shcherbich & C. Yamashiro. 2014. Ambient temperature influences adult size and life span in jumbo squid (*Dosidicus gigas*). Canadian Journal of Fisheries and Aquatic Sciences, 2015, 72(3): 400-409, 10.1139/cjfas-2014-0386

Bazzino, G., 2001. Análisis de los efectos ambientales sobre la distribución y abundancia del calamar *Illex argentinus* (Cephalopoda, Ommastrephidae) en la Zona Común de Pesca Argentino-Uruguaya. Tesis para optar al grado de Magíster en Ciencias con Mención en Pesquerías. Universidad de Concepción. Chile: 116 pp.

Benites, C. 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. En: Alvaro E. Tresierra Aguilar (Ed) Anales I Congreso Nacional de Biología Pesquera 28 de junio al 01 de julio 1984, Trujillo-Perú: 10-16.

Benites, C. & V. Valdivieso. 1986. Resultados de la pesca exploratoria de 1978/80 y desembarque de cefalópodos pelágicos en el litoral peruano. Bol. Inst. Mar Perú, 10(5): 139 pp.

Boyle, P.R. & S.V. Boletzky. 1996. Cephalopod populations: definitions and dynamics. Philosophical Transactions of the Royal Society of London Series B, 351: 985–1002.

Castillo, R. & A. Aliaga. 2000. Distribución de los recursos pelágicos del 25 al 27 de octubre 1999. Crucero BIC Jose Olaya Balandra. Inf. Inst. Mar Perú. N°156: 37-42.

Castillo, R., S. Peraltilla, A. Aliaga, M. Flores, M. Ballon, J. Calderón & M. Gutierrez. 2009. Protocolo técnico para la evaluación acústica de las áreas de distribución y abundancia de recursos pelágicos en el mar peruano. Inf. Inst. Mar Perú. Vol.32: 7-28.

Clarke, R., O. Paliza & A. Aguayo. 1998. Sperm whales of the southeast pacific. Part IV: fatness, food and feeding. Investigations on Cetacea. Edited by G. Pilleri Vol. XXI, 1998: 53-195

Clarke R. & O. Paliza. 2000. The Humboldt current squid *Dosidicus gigas* (Orbigny, 1835). Rev Biol Mar Oceanogr 35:1-38

Ehrhardt N, P. Jacquemin, F. Garcia, G. Gonzalez, J.M. Lopez, J. Ortiz & A. Solis, 1983. On the fishery and biology of the giant squid, *Dosidicus gigas*, in the Gulf of California, México. *In* Advances in assessment of world cephalopod resources, Edited by JF Caddy. FAO Fishery Technical Paper (231): 306-40.

Field, J. C., K. Baltz, A.J. Phillips & W. Walker. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. CCOFI Rep. 48:131-146.

Field, J.C., C. Elliger, K. Baltz, G.E. Gillespie, W.F. Gilly, R.I. Ruiz-Cooley, D. Pearse, J.S. Stewart, W. Matsubu & W. Walker. 2013. Foraging ecology and movement patterns of jumbo squid (*Dosidicus gigas*) in the California Current System. Deep Sea Res. Part II Top. Stud. Oceanogr. 95: 37–51. doi:10.1016/j.dsr2.2012.09.006

Fisheries Agency of Japan 1999. Report of the Kaiyo Maru cruise for study on the resourses of two Ommastrephid squids, *Dosidicus gigas* and *Ommastrephes bartrami*, in the Pacific Ocean, during September 11 – December 24,1997: 207 pp.

Fisheries Agency of Japan. 2009. The R/V Kaiyo Maru 2007 Cruise Report Japan and Peru joint study of the Jumbo Flying squid, *Dosidicus gigas*, in the Eastern Pacific Ocean, during September 11 – December 24,1997. 2009: 177 pp.

Fisheries Agency of Japan. 2012. The R/V Kaiyo Maru 2011 Reseach Cruise Report, Recuitment of the Jumbo Flying squid, *Dosidicus gigas*, in the EEZ of Peru and the off Peru waters from December 2011 to Febrary 2012: 201 pp.

Flores, M., S. Vera, R. Marcelo & E. Chirinos. 1994. Estadísticas de los desembarques de la pesquería marina peruana 1983-1992. Inf. Inst. Mar Perú 104: 200 p.

Flores, M., M. Segura y A. Aliaga. In press. Biomasa y distribución del calamar gigante (*Dosidicus gigas*) aplicando la metodología hidroacústica en el mar peruano**.** Bol. Inst. Mar Peru (in press): xxp

Gilly, W.F., U. Markaida, C.H. Baxter, B.A. Block BA, A. Boustany, L.D. Zeidberg, K. Reisenbichler, B. Robison, B. Bazzino & C. Salinas. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. Marine Ecology Progress Series. 324: 1–17.

Guevara-Carrasco, R., C. Yamashiro, L. Mariategui & J. Arguelles. In press. Aspectos relevantes en la ordenación pesquera del calamar gigante o pota (*Dosidicus gigas*) en el Perú. Bol. Inst. Mar Peru (in press): xxp

Ibáñez, C., H. Arancibia & L. Cubillos. 2008. Biases in determining the diet of jumbo squid *Dosidicus gigas* (D’ Orbigny 1835) (Cephalopoda: Ommastrephidae) off southern-central Chile (34°S–40°S). Helgol Mar Res 62: 331-338

Ibañez, C., 2010. Estructura poblacional y diversidad genética de calamares con historias de vida contrastantes en el sistema de corrientes de Humboldt. Tesis para optar al grado de Doctor en Ciencias con mención en Ecología y Biología Evolutiva: 130p.

Ibáñez, C., L. Cubillos, R. Tafur, J. Argüelles, C. Yamashiro & E. Poulin. 2011. Genetic diversity and demographic history of *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in the Humboldt Current System. Marine Ecology Progress Series.

IMARPE. 2015. Crucero de investigación del calamar gigante, CR. 1501-02, 20 enero al 09 febrero de 2015. BIC José Olaya Balandra - Zona Norte, BIC Humboldt-Zona Sur. Informe Ejecutivo, IMARPE, Callao: 54 pp (http://www.imarpe.pe/imarpe/archivos/informes/CruceroInvestigacionCalamarGigante.pdf)

IMARPE. 2015a. Situación del calamar gigante durante el 2014 y perspectivas de pesca para el 2015. Informe interno IMARPE, Callao, marzo 2015: 10pp (http://www.imarpe.pe/imarpe/archivos/informes/imarpe/inf_calmar_2014_pers2015.pdf)

IMARPE and Fisheries Agency of Japan. 2013. Crucero de Investigación Conjunta del Calamar Gigante *Dosidicus gigas* - BIC Kaiyo Maru 2011-2012 (16 de diciembre del 2011 al 19 de enero de 2012). En: Mitsuo Sakai y Carmen Yamashiro (Eds) Informe Final Instituto del Mar del Perú/Fisheries Agency of Japan: 77 p.

Johannesson, K. & A. Robles. 1977. Echo surveys of Peruvian anchoveta. Rapp. P.-V. Réun. Cons. Int. Explor. Mer., 170: 237-244.

Keyl, F., J. Argüelles & R. Tafur. 2010. Inter-annual variability of population structure, age and growth of *Dosidicus gigas* in the Peruvian EEZ. ICES J Mar Sci. doi:10.1093/icesjms/fsq167

Kreuzer, R. 1984. Cephalopods: handling, processing and products. FAO Fisheries Technical Paper (254): 108 pp.

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: 89-105. In: Okutani, T. (Ed.), Contributed papers to International Symposium on Large Pelagic Squids, Tokyo, July 18-19, 1996. JAMARC: 269 pp.

Liu B., Chen X., Chen Y., Tian S., Li J., Fang Z., Yang M.. 2013. Age, maturation, and population structure of the Humboldt squid *Dosidicus gigas* off the Peruvian Exclusive Economic Zones. Chinese Journal of Oceanology and Limnology. Vol. 31 (1): 81-91.

Lorrain, A., J. Argüelles, A. Alegre, A. Bertrand, J.M. Munaron, P. Richard & Y. Cherel. 2011. Sequential Isotopic Signature Along Gladius Highlights Contrasted Individual Foraging Strategies of Jumbo Squid (*Dosidicus gigas*). PLoS One 6, e22194.

MacLennan, D., & J. Simmonds. 1992. Fisheries Acoustics. London, Chapman and Hall Eds.: 325 pp.

Mariátegui, L. y A. Taipe. 1996. Distribución y abundancia relativa del calamar gigante (*Dosidicus gigas*) en el Perú. Inf. Prog. Inst. Mar Perú, 34: 3-27.

Markaida, U. & O. Sosa-Nishizaki. 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. Journal of the Marine Biological Association of the United Kingdom, 83: 1–16.

Markaida, U., 2006. Food and feeding of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters after the 1997–98 El Nino event. Fisheries Research 79: 16–27.

Masuda, S., K. Yokawa, A. Yatsu & S. Kawahara. 1998. Growth and population structure of *Dosidicus gigas* in the Southeastern Pacific. In: Okutani, T. (Ed.). Large Pelagic Squid: 107-118.

Nesis, K.N., 1970. The biology of the giant squid of Perú and Chile, *Dosidicus gigas*. Oceanology 10, 108-118.

Nesis, K.N., 1983. *Dosidicus gigas*. In Boyle, P.R. (Ed.), Cephalopod Life Cycles. Volume 1. Academic Press, London, 215-231.

Nigmatullin, Ch. M., K.N. Nesis & A.I. Arkhipkin. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). Fisheries Research 54, 9-19.

Plummer, M. 2013. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. DSC 2003 Working Papers: 8p (http://www.ci.tuwien.ac.at/Conferences/DSC-2003)

Roper, C.F.E., M.J. Sweeney & C.E. Nauen 1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fishery Synopsis 125: 277 pp.

Rosas-Luis, R., R. Tafur-Jimenez, A.R., Alegre-Norza, P.R. -Valderrama, R.M. Cornejo-Urbina, C.A. Salinas-Zavala & P. Sánchez. 2011. Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria lucetia*) in the Humboldt Current System off Peru. Sci. Mar. 75: 549–557.

Rosas, R, 2007. Descripción de la alimentación del calamar gigante *Dosidicus gigas* D’Orbignyi, 1835 en la costa occidental de la Península de Baja california. Tesis Para optar el grado de Maestro en Ciencias. La Paz, Baja California: 84 p.

Rubio R. & C. Salazar. 1992. Prospección pesquera del calamar gigante (*Dosidicus gigas*) a bordo del buque japonés “Shinko Maru 2” (04 de noviembre-17 de diciembre de 1989). Inf. Inst. Mar Perú, 103: 31 pp.

Ruiz-Cooley, R., D. Gendron, S. Aguiñiga, S. Mesnick & J.D. Carriquiry. 2004. Trophic relationship between sperm whale and squid using stable isotopes of C and N. Marine Ecology Progress Series 277: 275-283.

Sandoval, E., M. Uribe & P. Diaz. 2007**.** Population genetic structure of jumbo squid (*Dosidicus gigas*) evaluated by RAPD analysis. Fisheries Research 83: 113–118.

Sandoval-Castellanos, E., M. Uribe-Alcocer & P. Díaz-Jaimes. 2009. Lack of genetic differentiation among size groups of jumbo squid (*Dosidicus gigas*). Ciencias Marinas, 35(4): 419–428

Sandoval, E., M. Uribe & P. Diaz. 2010. Population genetic structure of the Humboldt squid (*Dosidicus gigas*, d'Orbigny, 1835) inferred by mitochondrial DNA analysis. Journal of Experimental Marine Biology and Ecology 385: 73–78.

Segura, M., R. , J. Rubio, A. Tello, M. Gutierrez & A. Aliaga. 1996. Crucero de investigaciones sobre el recurso calamar gigante o pota a bordo del BIC SNP-1. CR.9510-11. Inf. Prog. Inst. Mar Perú, 34: 29-65.

Seibel, B.A. 2011. Critical oxygen partial pressures and metabolic suppression in oxygen minimum zones. J Exp Biol 214: 326–336.

Seibel, B. A. 2013. The jumbo squid, *Dosidicus gigas* (Ommastrephidae), living in oxygen minimum zones II: Blood–oxygen binding. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 139–144. doi:10.1016/j.dsr2.2012.10.003

Shchetinnikov, A.S. 1989. Food spectrum of *Dosidicus gigas* (Oegopsida) in the ontogenesis. Zoologicheskii Zhurnal. 68, 28-39 (In Russian with English abstract).

Tafur, R., P. Villegas, M. Rabí, & C. Yamashiro. 2001. Dynamics of maturation, seasonality of reproduction and spawning grounds of the jumbo squid *Dosidicus gigas* Cephalopado: Ommastrephidae) in Peruvian waters. Fisheries Research 54: 33-50.

Tafur, R. & M. Rabí. 1997. Reproduction of the jumbo squid, *Dosidicus gigas* (Orbigny, 1835) (Cephalopoda: Ommastrephidae) off Peruvian coasts. Sci. Mar., 61(Supl. 2): 33-37.

Tafur R, F. Keyl, & J. Argüelles. 2010. Reproductive biology of jumbo squid *Dosidicus gigas* in relation to environmental variability of the northern Humboldt Current System. Mar Ecol Prog Ser 400: 127–141

Tafur, R., A. Perea & B. Buitron. In Press. Aspectos reproductivos de *Dosidicus gigas* “pota” en aguas peruanas. Bol. Inst. Mar. Perú (in press):

Ulloa, P., M. Fuentealba & V. Ruiz. 2006. Hábitos alimentarios de *Dosidicus gigas* (D' Orbigny, 1835) (Cephalopoda: Teuthoidea) frente a la costa centro-sur de Chile. R*e*vista Chilena de Historia Natural 79: 475-479.

Vinatea, J. E. 1965. Estudio cuantitativo del contenido estomacal del cachalote en el área de Pisco (1961 1963). Lima (PE), 1965: 101 p., 41 refs., Graf., Tab. Universidad Nacional Mayor de San Marcos. Bachiller en Ciencias Biológicas.

Wormuth, J.H. 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. Bull Scripps Inst Oceanogr 23

Wormuth, J. H. 1998. Workshop deliberations on the Ommastrephidae: A brief history of their systematics and a review of the systematics, distribution, and biology of the genera Martialia Rochebrune and Mabille, 1889, Todaropsis Girard, 1890, Dosidicus Steenstrup, 1857, Hyaloteuthis Gray, 1849, and Eucleoteuthis Berry, 1916. In Voss, N. A., M. Vecchione, R. B. Toll y M. J. Sweeney (Eds.), Systematics and biogeography of cephalopods. Vol. I. Smith. Contrib. Zool., 586 (II): 373-383.

Yamashiro, C., L. Mariátegui & A. Taipe. 1997. Cambios en la distribución y concentración del calamar gigante (*Dosidicus gigas*) frente a la costa peruana durante 1991-1995. Inf. Prog. Inst. Mar Perú, 52: 3-40.

Yatsu, A., R. Tafur & C. Maravi.1999. Embryos and Rhynchoteutian Paralarvae of the Jumbo Flying Squid *Dosidicus gigas* (Cephalopoda) Obtained Through Artificial Fertilization from Peruvian Waters. Fish Sci (Tokyo) 65: 904-908

Yatsu, A., K. Yamanaka & C. Yamashiro. 1999a. Tracking experiments of the jumbo flying squid *Dosidicus gigas* with an ultrasonic telemetry system in the Eastern Pacific Ocean. Bull. Nat. Res. Inst. Far Seas Fish. 36: 55-59.

Zeidberg, L.D. & B. H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc. Natl. Acad. Sci. 04:12948–12950.