# A HYPOTHESIS ON RANGE EXPANSION AND SPATIO-TEMPORAL SHIFTS IN SIZE-AT-MATURITY OF JUMBO SQUID (*DOSIDICUS GIGAS*) IN THE EASTERN PACIFIC OCEAN

FRIEDEMANN KEYL
Centre for Tropical Marine Ecology
Fahrenheitstr. 6, 28359
Bremen, Germany
friedemann.keyl@zmt.uni-bremen.de

MATTHIAS WOLFF
Centre for Tropical Marine Ecology
Fahrenheitstr. 6, 28359
Bremen, Germany

JUAN ARGÜELLES, LUÍS MARIÁTEGUI, RICARDO TAFUR
Instituto del Mar del Perú (IMARPE)
Esquina Gamarra y General Valle s/n
Casilla postal 22
Chucuito, Callao
Perú

CARMEN YAMASHIRO
Instituto del Mar del Perú (IMARPE)
Esquina Gamarra y General Valle s/n
Casilla postal 22
Chucuito, Callao
Perú

## ABSTRACT

*Dosidicus gigas* is a fast growing predator in the eastern Pacific Rim with a high energy demand. Since 2000, it has been found in waters beyond its until-then-known northern and southern distribution limits. At the same time, specimens in the southern hemisphere were observed to reach maturity at significantly larger sizes. Spatio-temporal differences in temperature and food abundance may explain population changes in maturation, growth, and migration. Size-at-maturity depends on temperature and food availability, meaning jumbo squid will mature at smaller sizes under warm conditions and at larger sizes that can migrate longer distances in cool conditions. In this paper, we present the hypothesis that the present invasion of jumbo squid into formerly uninhabited areas was the result of a combination of favorable environmental conditions and fishery impacts: the regime shift from warm to cool water following a strong La Niña/El Niño combined with the fisheries' impact on competitors and predators of *D. gigas* opened up a previously unavailable niche, or "loophole," and allowed for the present spatial expansion of jumbo squid.

## INTRODUCTION

The jumbo squid, *Dosidicus gigas*, is a migratory and voracious predator of the eastern Pacific Ocean with high abundances in the southern area of the California Current system and in the northern region of the Humboldt Current system (Roper et al. 1984). It has a high energy demand that is satisfied by unspecific feeding upon prey items that are 5% to 25% the size of its dorsal mantle length (ML), although bigger prey have been reported. In cannibalistic feeding, a commonly observed behavior for jumbo squid, prey size may reach up to 87% of the predators' ML (Markaida and Sosa-Nishizaki 2003). Jumbo squid hunt in small groups (Nigmatullin et al. 2001) and, although they are extreme generalists, it has been shown that myctophids and euphausiids often comprise an important percentage in the diet of juveniles and adults (Markaida 2006a; Blasković et al. 2007). Large females can have as many as 32 million eggs (normally 0.3–13 million eggs are found), which is the highest fecundity among cephalopods (Nigmatullin et al. 2001). Although not universally accepted (Masuda et al. 1998), *D. gigas*, like most other cephalopods, is thought to exhibit "cephalopod senescence" (Anderson et al. 2002) and is semelparous, that is, it does not regress developed reproductive organs but dies after the first spawning or the first spawning sequence (Nigmatullin et al 2001). Like other cephalopods, it does not develop a true larval phase but hatches after three to 10 days as a paralarva (Yatsu et al. 1999), a life stage very similar to the subsequent adult stage. Jumbo squid have a monthly growth rate of up to 8 cm in mantle length (ML) during the paralarvae and the following juvenile stages, and grow up to 6 cm per month in later stages. This is the highest growth rate reported for all cephalopod species (Nigmatullin et al. 2001; Markaida et al. 2005) and enables jumbo squid to reach the reported maximum mantle lengths of up to 120 cm in a lifespan of just a few to 18 months (Nigmatullin et al. 2001).

Until the end of the last millennium, the jumbo squid's northern and southern distribution limits were found at around 30°N and 40°S, with the highest abundances located in the Gulf of California and in waters off Peru (Nigmatullin et al. 2001). A recent RAPD-genetic analysis of eight locations in Mexico, Peru, and Chile indicated that the jumbo squid sub-populations from the two hemispheres are genetically separated, probably because the equatorial currents and counter-currents form a natural barrier (Sandoval-Castellanos et al. 2007).

Various traits of its life history, like shifts in size-at-maturity, cannibalism, and range expansion, give *D. gigas* an extremely plastic response to the highly variable oceanic habitats within the eastern boundary upwelling systems.

Jumbo squid size-at-maturity is highly variable and several authors (e.g., Nesis 1983; Nigmatullin et al. 2001) have proposed three different size-at-maturity strategies in its distribution in the eastern Pacific Ocean (EPO): a

group found in the center of its EPO distribution that matures at a small size; a group throughout the whole distribution area that matures at a medium size; and a group in the northern and southern distribution limits that matures at large size. In Peruvian waters, these groups have not yet been identified from the available oceanic industrial and coastal artisanal fisheries data. Only a small-maturing group and a large-maturing group, which generally correspond to the medium- and the large-sized groups classified by Nigmatullin et al. (2001), can be distinguished (fig. 1) and appear to be both spatially and temporally separated (Argüelles et al. 2008). The terms "small" and "large" in the present study refer to the two size-at-maturity groups found in the Peruvian waters; when we refer to Nigmatullin et al.'s (2001) group classification, this is explicitly mentioned. In the Peruvian exclusive economic zone (EEZ), from 1989 through 1999 (except 1992–93) only specimens of the small size-at-maturity group were caught, whereas, after a transition period in 1999–2000, only specimens thought to belong to the large group were caught (fig. 1).

Statolith analyses revealed that the longevity of mature individuals collected by observers in the industrial fishery in the Peruvian EEZ ranged from around 120 to 350 days according to their size (Masuda et al. 1998; Argüelles et al. 2001). A temporal change in size-at-maturity has also been found for the jumbo squid population in the Gulf of California, where, in a three-year period after the 1997–98 El Niño, the size-at-maturity varied considerably from large to small or medium (Markaida 2006b; Bazzino et al. 2007). Although these groups may belong to genetically different sub-populations (Nesis 1983), no work has been published on the origin or an underlying cause for the existence of these groups.

Cannibalistic feeding is a common behavior among cephalopod species (Amaratunga 1987) and this has been confirmed in stomach content analyses of *D. gigas* from the Gulf of California (Markaida 2006a) and Peruvian waters (Blasković et al. 2007). Among other things, cannibalism reduces intraspecific competition for food and mating under conditions of reduced food availability or very high population densities, allows larger specimens to maintain their food intake over time, and therefore, to increase their fitness (Polis 1981). The cannibalistic weight percentage of all stomach contents of specimens caught by the industrial fishery on jumbo squid in Peruvian waters from 2004 to 2006 ($n$ = 1930; 30–112 cm ML) reached 75% (IMARPE unpubl. data). Although this high rate of cannibalism may be partly due to stress during fishing (Markaida and Sosa-Nishizaki 2003; Ibáñez et al. 2008) and although it may reflect a systematic bias because only larger individuals were captured, it suggests a "population energy storage" strategy: energy is built up during favorable ecosystem conditions by increasing

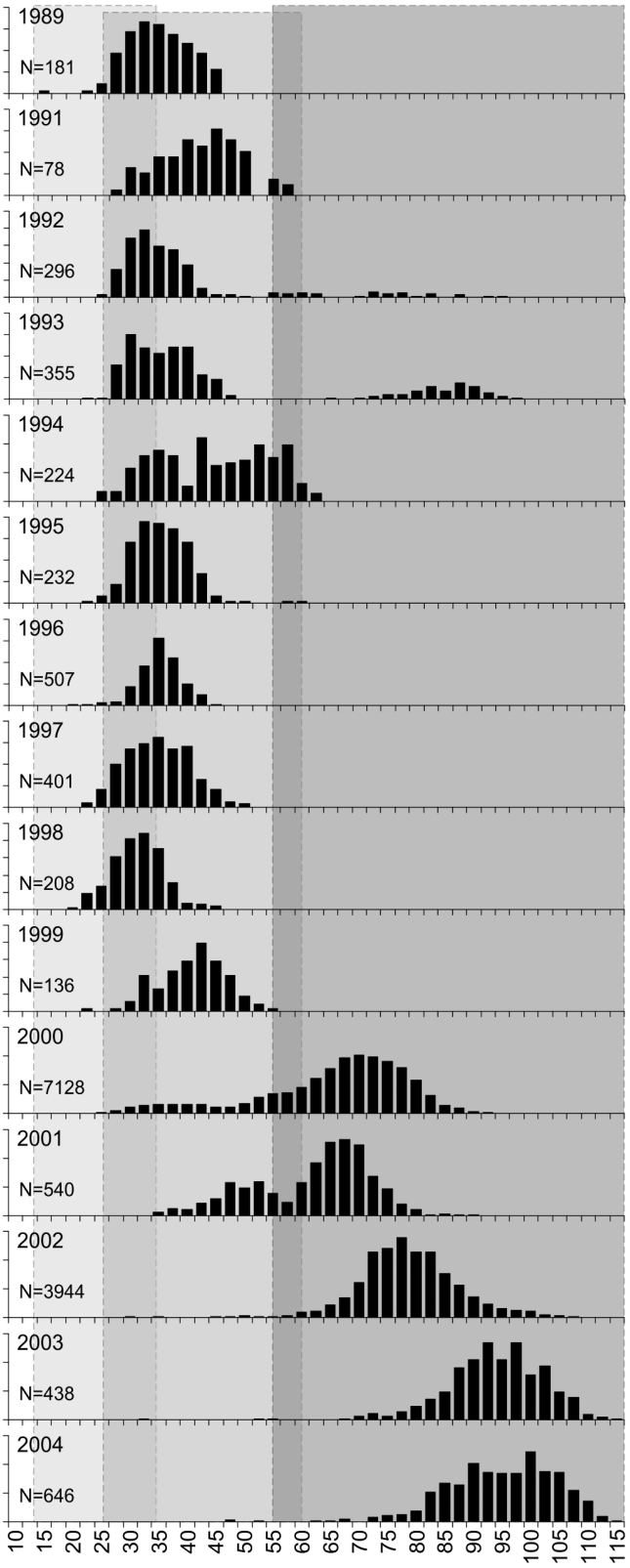


Figure 1: Occurrence of sizes (ML [cm]) of mature females by industrial jig fishery in the Peruvian EEZ; shaded boxes indicate the three groups of size-at-maturity proposed by Nigmatullin et al. (2001); modified after Argüelles et al. 2008.

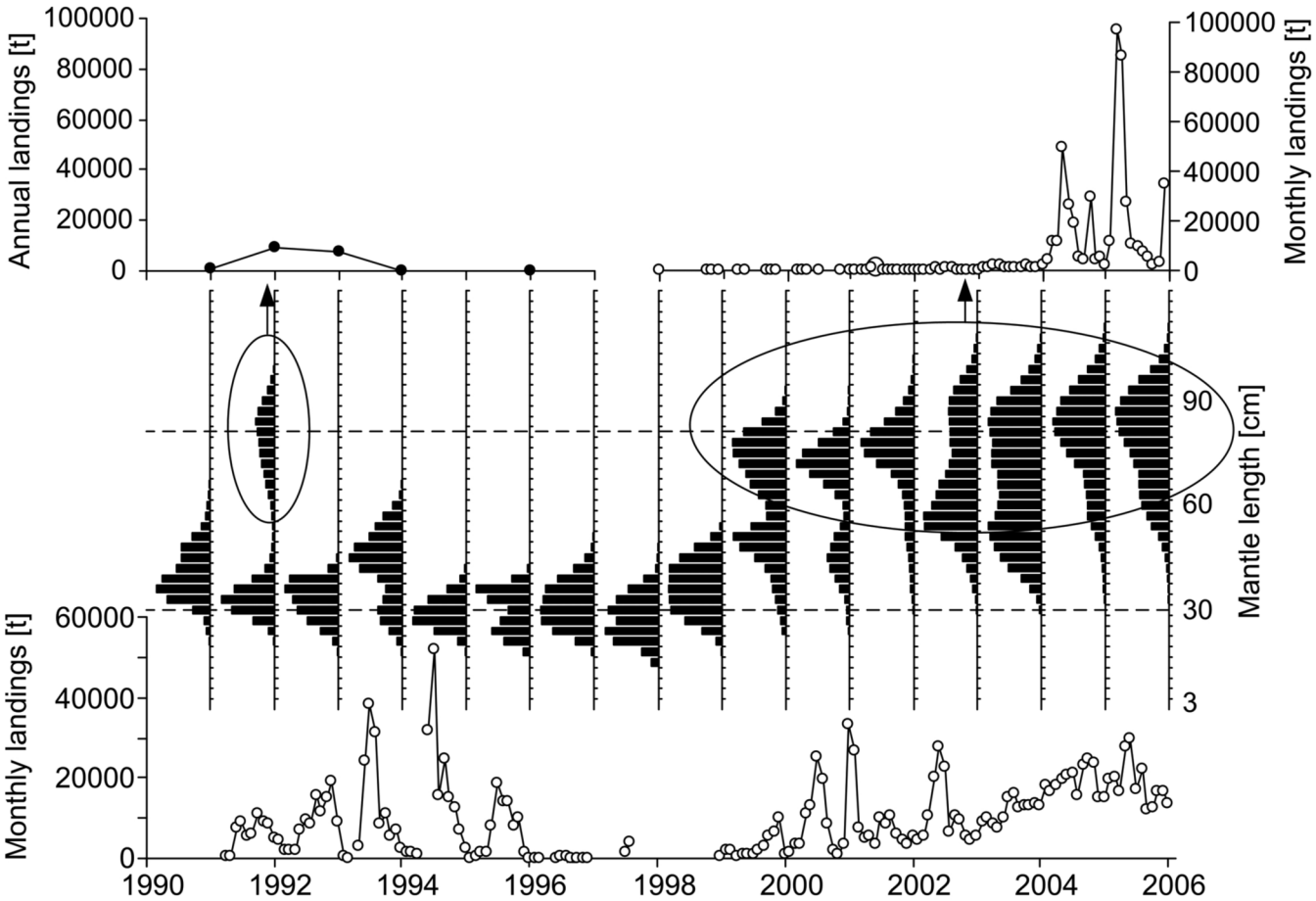


Figure 2: Temporal coincidence of high annual landings in Chilean regions IV (Coquimbo, ~30°S) to VIII (Bío-Bío, ~40°S, upper panel; filled circles: annual landings from 1991 to 97, open circles: monthly landings from 1998 to 2005) with the occurrence of the large specimen observed in the landings from the Peruvian EEZ in 1992 and from 2000 on (middle panel); lower panel: monthly landings of industrial and artisanal fishery in the Peruvian EEZ.

the number of individuals that can be reduced again by the larger individuals when the population is under ecological stress.

After the 1997–98 El Niño, a range expansion of jumbo squid was observed in the north Pacific Ocean (Zeidberg and Robison 2007; Staaf et al. 2008) and south Pacific Ocean (upper panel of fig. 2; fishery data of Chilean SENARPESCA, see web page: http://www.senarpesca.cl/). From 2002 to 2004, reported annual landings of jumbo squid from off Chile increased from 5500 t to nearly 300,000 t. This increase in landings partially resulted from the directed artisanal jig fishery for jumbo squid, but squid was mainly captured as increased bycatch of other fisheries employing different types of fishing gear (Ibáñez et al. 2008). After mass strandings in California in 2002 and sightings of *D. gigas* up to Alaska since 2002, the jumbo squid became an important target of the U.S. sport fishery (Hatfield and Hochberg 2006). This coincides with the steadily increasing biomasses as estimated from catch per unit of effort (CPUE) and acoustic surveys (IMARPE, unpubl. data) which have sustained the continuously increasing total allowable catch for the Peruvian fishery since 2000 (lower panel of fig. 2). At present, the northern and southern limits of jumbo squid distribution are 60°N and 50°S, respectively (fig. 3), although it is not clear if the expansion has ceased or will continue into new areas.

## THE FUNCTIONAL TRIAD MIGRATION-MATURATION-GROWTH

Because changes in population size structure, abundance, and distribution observed during the last decade seem to be related (fig. 2), we propose that individual migration, maturation, and growth are connected via a functional triad on a physiological and energetic basis: as a mobile and fast growing hunter, *D. gigas* has a high energy demand and available food has to change rapidly in quality and size while the squid grows from the planktonic paralarva to its final length in just a few months. Migration routes must thus change with the spatio-temporal occurrence of prey items as the nutritional needs of the squid change through different size classes.

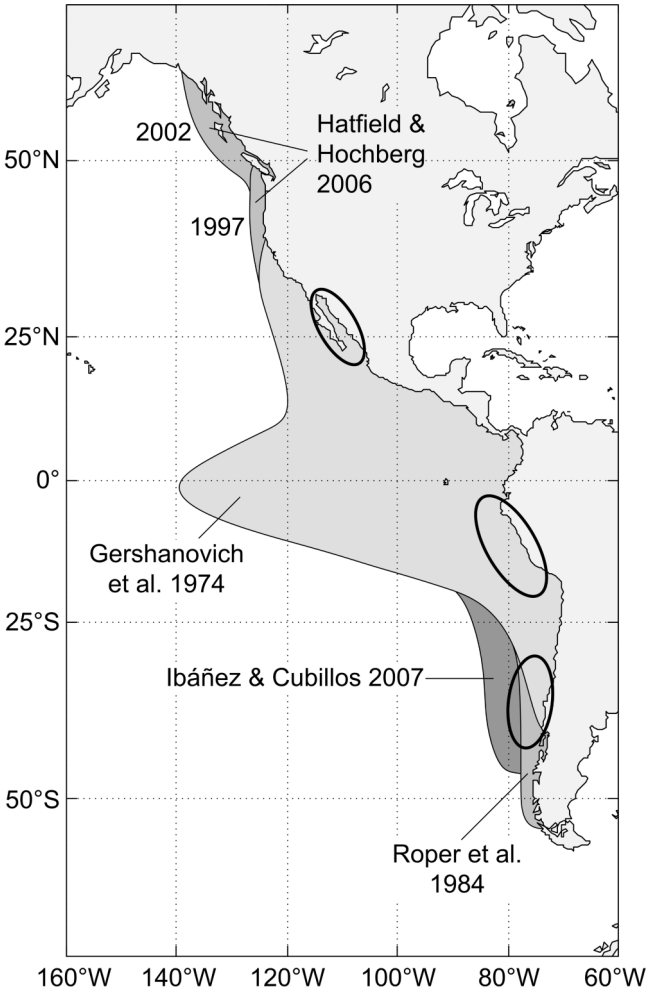


Figure 3: Distribution area of *Dosidicus gigas* according to different sources in different years indicating an extension of the range; ellipses show main fishing areas.

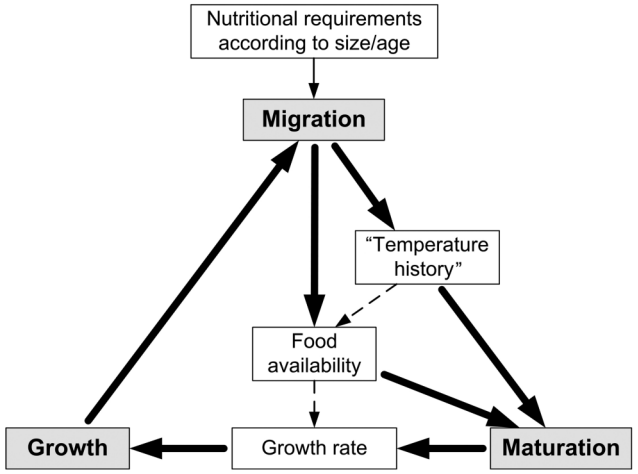


Figure 4: Scheme of the functional triad migration-maturation-growth: individual nutritional requirements lead to migration patterns that lead to a temperature history according to water masses passed, which controls the onset of maturity, that in turn controls growth rate and finally growth. Growth, i.e., the size of a specimen, again influences its migration; dashed interactions that have been reported for some cephalopod species (e.g., Pecl & Jackson 2006) have not been considered in the present hypothesis; further explanations in the text.

During the horizontal migration of up to 30 km per day (Gilly et al. 2006) and regular vertical migrations to depths of 1200 m (Nigmatullin et al. 2001), individuals pass through different water masses which leads to a unique temperature and nutrition history for each squid. We postulate that this history may govern the onset of jumbo squid maturation by a specific, but unknown, number of day-degrees, as has been suggested for other cephalopods (Rodhouse 1998). Environmental variables, temperature, and food availability have also been described as factors that control cephalopod maturation. High nutrition levels and low temperatures are known to cause late maturation and low nutrition levels and high temperatures cause early maturation (Mangold 1987). Following this reasoning, the individual temperature and nutrition history would thus determine the onset of maturation, which in turn controls the maximum size the individual can attain (fig. 4) because *D. gigas* is semelparous and dies after its first reproduction season (Nigmatullin et al. 2001). Consequently, groups of *D. gigas* that differ in size-at-maturity and final size may have experienced different environmental conditions with respect to temperature and nutrition and may have therefore migrated along different routes.

In Peruvian waters, the available data for mature females indicate that there are two size-at-maturity groups and do not support Nigmatullin et al.'s (2001) three-group hypothesis (fig. 1). The size distributions of immature and mature females and males in Peruvian landings suggest the existence of more groups in the population (fig. 2, middle panel). However, since these landings are composed of mature and immature individuals of possibly different cohorts (Tafur et al. 2001) they should not be confused with the different groups of size-at-maturity. Argüelles et al. (2001) found that individuals of the large size-at-maturity group are older than those of the small group, which agrees with our hypothesis.

## Size-at-maturity groups

Very few studies have examined whether genetic, abiotic, biotic, or a mixture of these factors are responsible for observed differences in sizes-at-maturity of jumbo squid (Nesis 1983; Nigmatullin et al. 2001). This suggests that the underlying mechanism proposed in our study, which links physiological and ecological/environmental factors, has not been considered.

If, as the Peruvian fishery data suggest (figs. 1 and 2), mature specimens were divided into small/early and big/late maturing groups, the small group would be at a disadvantage since the higher *relative* energy a small in-

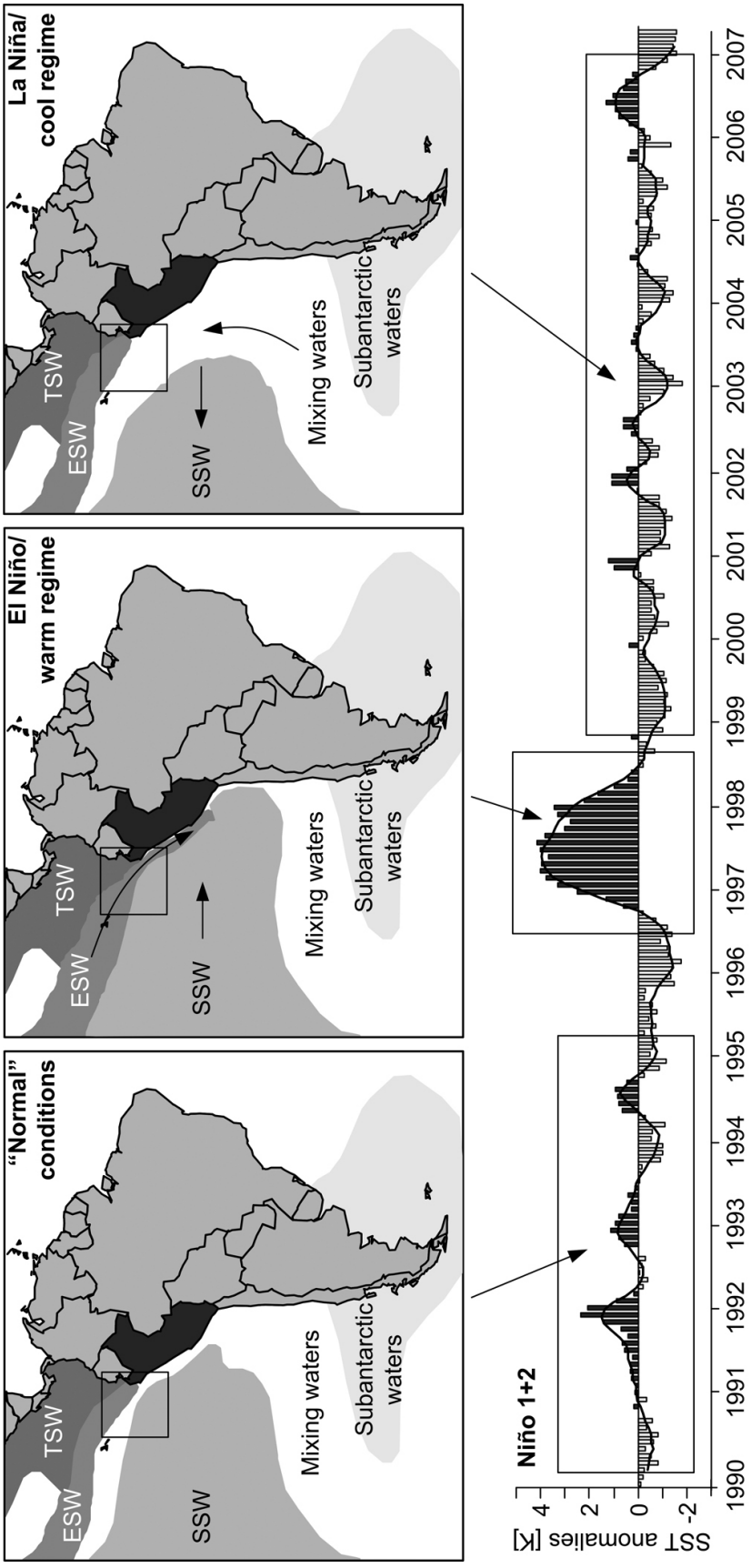


Figure 5: Schematic illustration of the "mean" location of water masses during different times/regimes in the South Eastern Pacific obtained from satellite SST data and oceanographic data collected during research and monitoring cruises of the IMARPE (after Morón and Sarmiento 1999; Ahumada et al. 2000; O. Morøn, pers. commun. IMARPE); ESW: equatorial surface waters; TSW: tropical surface waters; SSW: subtropical surface waters; the squares in the sketches show the Niño 1+2-region; lower panel shows SST-anomalies of the Niño 1+2-region.

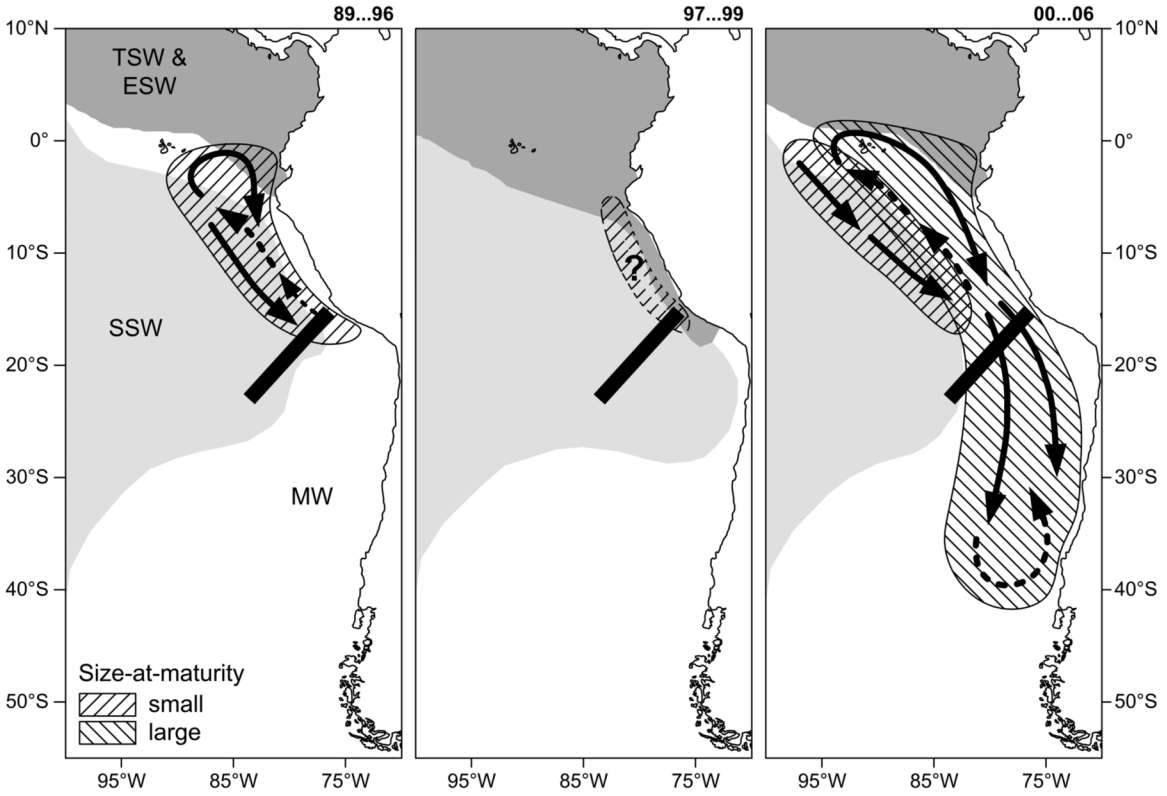


Figure 6: Scheme of distribution areas/fishing grounds and proposed migration routes of *D. gigas* in the SE Pacific during the "normal" period from 1989 to 1996, during and after El Niño 1997 to 1999 and from 2000; hatched areas: distribution areas/fishing grounds of *D. gigas*; black arrows: assumed migration patterns of *D. gigas*; broken black arrows: assumed paralarval movement; dark grey area: tropical and equatorial surface waters (TSW & ESW); light grey area: subtropical surface waters (SSW); black bars: sketch of Nazca Ridge.

dividual invests into reproduction yields a lower reproductive output (Pecl and Jackson 2006; Argüelles and Tafur 2007). Additionally, small individuals have no access to larger prey or conspecifics at higher trophic levels, as do the larger specimens. On the other hand, smaller individuals may benefit under conditions of low food availability, as individually they invest less *absolute* energy into reproduction and because they are capable of feeding on smaller, more numerous food items at lower trophic levels. An advantage of the small size-at-maturity group is also its shorter generation time, so that lower individual reproduction adds up to a high population reproduction per unit of time. Moreover, the higher population turnover rate decreases the mean trophic level of the population as small individuals predominate, allowing it to feed at the more productive lower trophic levels.

Based on the above, we propose that the two groups have opposite life-history responses to two basic ecosystem conditions of the Humboldt Current system (HCS). The small size-at-maturity strategy ensures that the population survives during warm periods with low food availability, while the big size-at-maturity strategy allows for maximizing individual fitness during cool periods with abundant prey.

**Migration pattern and observed range expansion**

In the HCS these conditions are related to water masses characterized by different sea surface temperatures (SST) and salinities that change their locations off the coast of Peru according to large-scale oceanographic and atmospheric conditions and the resulting intensification or weakening of currents (fig. 5). In the 1990s until the beginning of 1996, the EPO showed moderate changes between positive and negative SST anomalies, which resulted in the limit between cool mixing waters (MW) and warmer subtropical surface waters (SSW) occurring inside the Peruvian EEZ. During the strong El Niño of 1997–98 the equatorial undercurrent (EUC) increased in strength, transported very warm equatorial surface waters southward, pushed the SSW closer to the Peruvian coast, and weakened the highly productive coastal upwelling cells. From 1999 on, a general cool regime entered the eastern Pacific Ocean, characterized by intense upwelling, a strong Humboldt Current and weak EUC. It produced negative SST anomalies in the Peruvian EEZ by pushing the limiting SSW farther westward and outside the Peruvian EEZ, and by allowing the formation of a broad zone of cool, nutrient-rich MW off the Peruvian coast

(Morón and Sarmiento 1999; O. Morón, pers. commun. IMARPE).

We assume that changes in water mass distributions lead to changes in the distribution area and main fishing grounds of *D. gigas* (fig. 6). The small size-at-maturity group found in the official landings data for the early 1990s is assumed to be associated with the boundary between the cool MW and warmer SSW and to move back and forth between the two water masses. Migration to the southern part of the HCS during that period seems to be restricted to some years and a low number of individuals. Although exact mechanisms are not known, this may result from the location of the SSW relative to the Nazca Ridge (black bars in fig. 6) that possibly acts as a barrier for smaller *D. gigas*, preventing them from migrating to colder waters in the south. This barrier may have its origin in bathymetric and oceanographic conditions different from those farther south and farther north off the Peruvian coast (Wolff et al. 2003; Shaffer et al. 2004), leading to significantly weaker upwelling and to less productivity in coastal areas farther south (Longhurst 1995).

Further evidence for this is found in the data from the industrial fishery inside the Peruvian EEZ which indicate that the resource is mainly distributed north of the Nazca Ridge (Taipe et al. 2001). With DMSP-OLS images it is possible to assess night-time activities of the industrial jumbo squid jigging fleets as they use strong lights to attract their target (Waluda et al. 2004). A night-time light image integrating the cloud-free nights in 2003 (fig. 7) shows that just south of the Nazca Ridge no jig fishery has occurred this year.

Since 1999, the size of the individuals in the landings reported to Peruvian authorities increased due to the displacement of the limit of the two water masses farther offshore and outside the Peruvian EEZ (fig. 5). Inside the Peruvian EEZ the cool, nutrient-rich MW were found, and with these the big size-at-maturity group developed that was reported to national Peruvian fishery authorities. Since then, the limit between the warmer SSW and the cooler MW has been outside the 200-mile border and, according to our hypothesis, the small size-at-maturity group should be found there. Night-time satellite images suggest that the international jigging fleet has been operating outside the EEZ at all times (Waluda et al. 2004; IMARPE, unpubl. data) but no data on catches and population structure are available. Preliminary investigations of more recent night-time images at IMARPE and the night-time lights image of 2003 (fig. 7) suggest that the bigger part of the total industrial fishing effort is applied outside the EEZ.

Preliminary results from IMARPE's October–November 2007 research cruise, 0710–11, support this hypothesis. During the survey that covered the east-west trajectory from 30 nm to 350 nm off the northern Peruvian coast (4°S to 8°S), all mature individuals (72 to 98 cm ML; $n$ = 5) fished by trawl net and manual jigging inside the EEZ belonged to the large size-at-maturity group, and those outside it (22 to 42 cm ML; $n$ = 18) to the small group. This suggests that the large size-at-maturity group occurs mostly inside the EEZ and the small size-at-maturity group outside the EEZ because of the new water mass distribution. We propose that larger animals are restricted from reaching the warmer waters now found outside the EEZ because they require higher nutrition levels than these waters can provide. Individuals of the small group moving to cooler water masses inside the EEZ become part of the large size-at-maturity group as a consequence of the conditions of their new environment. This leads to a separation of the

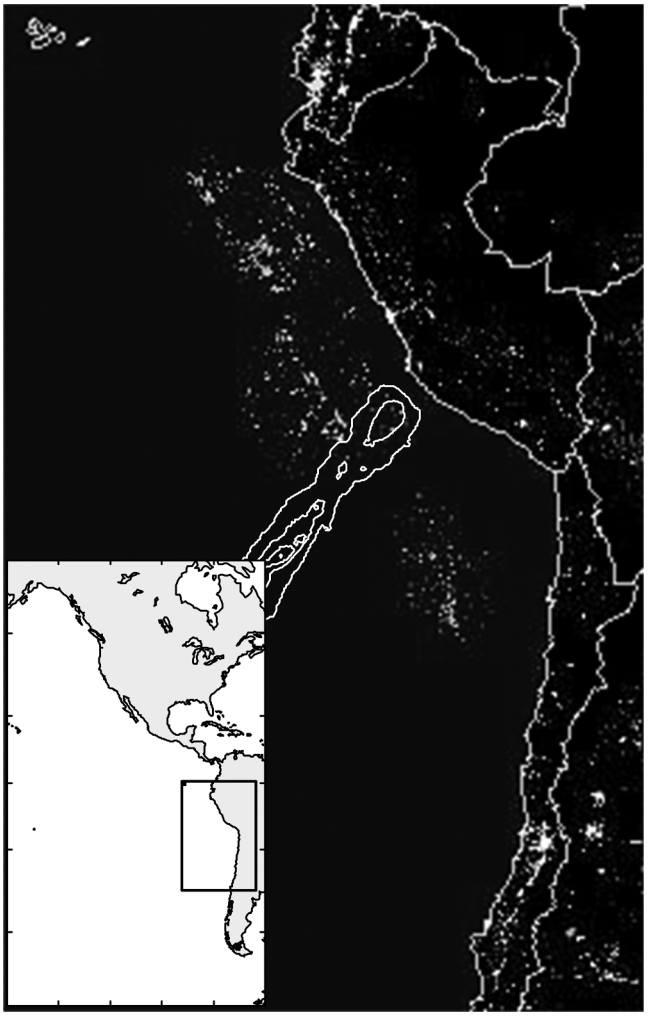

Figure 7: Integrated nighttime lights image of 2003 basing on visible and infrared radiation satellite data; white points off Peru and Chile indicate lights employed during nighttime fishing activity of the industrial jig fishery (modified after National Geophysical Data Center; http://www.ngdc.noaa.gov/dmsp/); Nazca Ridge is shown by depth lines in 1000 m intervals.

two size-groups that helps small individuals avoid falling prey to larger conspecifics.

The barrier formed by the Nazca Ridge and the water-masses ceases to exist with the retraction of the SSW from the coast, enabling parts of the population to migrate upstream along the Humboldt Current to Chilean waters. In the area from 30°S to 40°S where the Humboldt Current departs from the Chilean coast, they become vulnerable to fisheries again and are caught in large quantities. Clarke and Paliza (2002) proposed that mature jumbo squid may spawn in this area, but to our knowledge no one has yet reported paralarvae in Chilean waters. It is unknown whether spawning occurs in this area, or if the same individuals return to warmer waters off Peru to spawn, or die without spawning. However, periodic mass strandings in southern Chile have been reported (Ibáñez and Cubillos 2007). Few jumbo squid are fished in waters off northern Chile inside the EEZ (SENARPESCA data), however, in 2003 the international jigging fleet operated outside the EEZ (fig. 7). Again, the exact reason for this remains unclear but may result from the environmental conditions mentioned before. The changing intensities of the oceanic and a coastal branch of the northward flowing Humboldt Current in this area in different periods (Blanco et al. 2002) may also contribute to the observed distribution patterns.

## RANGE EXPANSION OF *D. GIGAS*: WHY NOW?

Although jumbo squid have never before been sighted as far north as Alaska, nor has the Chilean fishery reported such high landings since 2003, range expansions have been observed before in both hemispheres (Hatfield and Hochberg 2006; Ibáñez and Cubillos 2007; Staaf et al. 2008). Thus the question arises: why is the present range expansion so much stronger? We assume that both environmental variability and the indirect effect of fishery pressure in the HCS and the CCS affect the range expansion.

The last decade has seen a rare succession of environmental phenomena: after the strong La Niña/El Niño combination from 1996 to 1998, a Pacific-wide regime shift from warm to cool occurred that can be observed in the SST-anomalies off Peru (lower panel of fig. 5). The La Niña/El Niño period is considered as a "system reset" that can allow rapidly reproducing species to move into environmental "loopholes," i.e., niches formerly occupied by other species (Bakun and Broad 2003). The "loopholes" in the EPO open after the La Niña/El Niño-"system reset" and are exceptionally accessible for *D. gigas* because cool-regime waters are nutrient rich. At the same time, fisheries have greatly reduced the abundance of *D. gigas* competitors, such as mackerels and hake, and predators, like sharks and marine mammals (Tam et al. 2008), in the last decades (Pauly and Palomares 2005; Lotze et al. 2008), but have probably not affected their prey as euphausiids and myctophids.

These have been found to be important in the diet of *D. gigas* in the CCS (Markaida et al. 2006a) and the HCS (Blasković et al. 2007; Taylor et al. 2008) and can rapidly build up vast biomasses. No exploitation of the most important myctophid in the HCS, *Vinciguerria lucetia*, is known (Froese and Pauly 2007), and there are no reports of human exploitation of euphausiids in the HCS. The biomass increase of *V. lucetia* since 2000 may have partially fueled the increased biomass of jumbo squid (fig. 8, IMARPE, unpubl. data). Pauly et al. (2002) suggested that the abundance of marine resources such as invertebrates and jellyfish have a strong positive response to fishery-caused reductions in their competitors and predators. These groups are fast growing species often considered suppressed under "normal" conditions.

Thus, it seems that the concurrence of favorable "loopholes" after a "system reset" and fishery-caused reductions in competitors and predators has enabled *D. gigas* to expand its range.

## CONCLUSION AND FINAL REMARKS

The proposed migration-maturation-growth triad can explain the observed changes in population structure, abundance, and distribution of jumbo squid in the eastern Pacific Ocean during the last decade. Direct experimental evidence to prove our hypothesis is still missing, however. Until now it has not been possible to keep *D. gigas* under controlled aquarium conditions and the longest reported period that an adult jumbo squid has survived in captivity is 12 days (Gilly, Hopkins Marine Station, pers. comm.); paralarvae have been reported to survive 10 days (Ichii et al. 2002). Nevertheless, experimental work in the laboratory should be conducted to verify—or falsify—that *D. gigas* maturation and growth depend on temperature and food, which Mangold (1987) suggests for cephalopods in general. Other support for the hypothesis could come from biometric and maturity data from the Japanese and Korean jumbo squid fisheries, believed to have been operating outside the Peruvian EEZ for as long as those operating inside.

We have concentrated our analysis on the Peruvian part of the HCS, and further studies should clarify if the proposed triad also explains the range expansion and change in population size structure of *D. gigas* in the Gulf of California and the Californian Current system of the northern hemisphere, which are subjected to similar environmental and—at least in the Gulf of California—fishery conditions.

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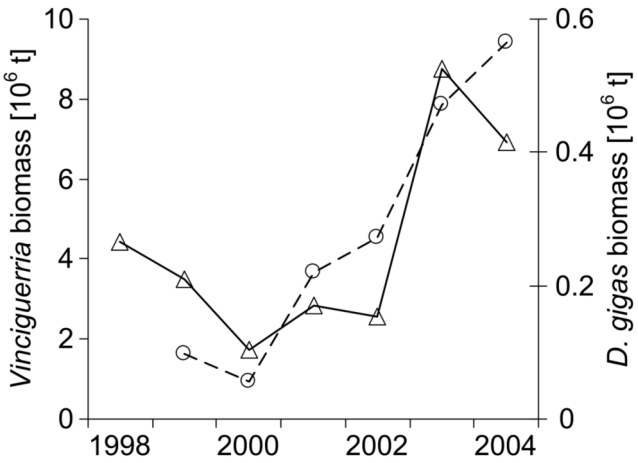


Figure 8: Biomasses of the myctophid *Vinciguerria* (triangles) and *D. gigas* (circles) in the Peruvian EEZ (IMARPE data from acoustic surveys).

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## REFERENCES

Ahumada, R., L. A. Pinto, and P.A. Camus. 2000. The Chilean Coast. *In* Seas at the Millennium: An Environmental Evaluation, Vol 1: Regional Chapters: Europe, The Americas and West Africa, C. R. C. Sheppard, ed. Amsterdam: Pergamon, 2422 pp.

Amaratunga, T. 1987. Population biology. *In* Cephalopod Life Cycles, P. R. Boyle, ed. London: Academic Press, pp. 239–252.

Anderson, R. C., J. B. Wood, and R. A. Byrne. 2002. Octopus Senescence: The Beginning of the End. J. Appl. Anim. Welf. Sci. 5:275–283.

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

Argüelles, J., and R. Tafur. 2007. Population structure, somatic and reproductive condition of *Dosidicus gigas* before, during and after ENSO events in the Humboldt Current System. In: J. Heine (Editor), CalCOFI Conference—Jumbo Squid Invasions in the Eastern Pacific Ocean. Californian Cooperative Oceanic Fisheries Investigations, Hubbs-SeaWorld Research Institute, San Diego, Cal, pp. 67.

Argüelles, J., R. Tafur, A. Taipe, P. Villegas, F. Keyl, N. Dominguez, and M. Salazar. 2008. Size increment of Jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. Prog. Oceanogr. DOI 10.1016/j. ocean. 2008. 10.003.

Bakun, A., and K. Broad. 2003. Environmental "loopholes" and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. Fish. Oceanogr. 12:458–473.

Bazzino, G., C. A. Salinas-Zavala, and U. Markaida. 2007. Variability in the population structure of jumbo squid (*Dosidicus gigas*) in Santa Rosalía, central Gulf of California. Cienc. Mar. 33:173–186.

Blanco, J. L., M. -E. Carr, A. C. Thomas, and P. T. Strub. 2002. Hydrographic conditions off northern Chile during the 1996–1998 La Niña and El Niño events. J. Geophys. Res. 107:3.1–3.15.

Blasković, V., A. Alegre, and R. Tafur. 2007. The importance of hake in the diet of the jumbo squid *Dosidicus gigas* in the north of the Peruvian zone (2005–2007). In: J. Heine (Editor), CalCOFI Conference—Jumbo Squid Invasions in the Eastern Pacific Ocean. Californian Cooperative Oceanic Fisheries Investigations, Hubbs-SeaWorld Research Institute, San Diego, Cal, pp. 67.

Clarke, R., and O. Paliza. 2002. La Pota y el Cachalote. *In* Bases Ecológicas y Socioeconómicas para el Manejo de los Recursos Vivos de la Reserva Nacional de Paracas, J. Mendo and M. Wolff eds. Lima, Perú: Universidad Nacional Agraria La Molina. pp. 119–124.

Froese, R., and D. Pauly (Editors). 2007. Fishbase. World Wide Web publication. www.fishbase.org, Version 04/2008.

Gershanovich, D. E., V. V. Natarov, and E. I. Cherny. 1974. Oceanologic bases as the forming up of the increased production areas in the Pacific Ocean. Trudy VNIRO 98:35–42

Gilly, W. F., U. Markaida, C. H. Baxter, B. A. Block, A. Boustany, L. Zeidberg, K. Reisenbichler, B. Robison, G. Bazzino, and C. Salinas. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. Mar. Ecol. Prog. Ser. 324:1–17.

Hatfield, E. M. C., and F. Hochberg. 2006. *Dosidicus gigas*: northern range expansion events. *In* B. Olson and J. Young (Editors), The Role of Squid in Pelagic Marine Ecosystems—GLOBEC-CLIOTOP WG3 Workshop, University of Hawaii, Manoa.

Ibáñez, C., and L. A. Cubillos. 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off central-south Chile. Sci. Mar. 71:123–128.

Ibáñez, C. M., H. Arancibia, and L. A. Cubillos. 2008. Biases in the diet of jumbo squid *Dosidicus gigas* (D' Orbigny 1835) (Cephalopoda: Ommastrephidae) off central southern Chile (34°S–40°S). Helgol Mar Res. DOI 10.007/s10152-008-0120-0

Ichii, T., K. Mahapatra, T. Watanabe, A. Yatsu, D. Inagake, and Y. Okada. 2002. Occurrence of jumbo flying squid *Dosidicus gigas* aggregations associated with the countercurrent ridge off the Costa Rica Dome during 1997 El Niño and 1999 La Niña. Mar. Ecol. Prog. Ser. 231:151–166.

Longhurst, A. 1995. Seasonal cycles of pelagic production and consumption. Prog. Oceanogr. 36:77–167

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson and J. B. C. Jackson. 2008. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science 312:1806–1809.

Mangold, K. 1987. Reproduction. *In* Cephalopod Life Cycles, P. R. Boyle ed. London: Academic Press. 157–200 pp.

Markaida, U., and O. Sosa-Nishizaki. 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. J. Mar. Biol. Assoc. U. K. 83:507–522.

Markaida, U., Rosenthal, J. J. C. and Gilly, W. F. 2005. Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. Fish Bull 103:219–226.

Markaida, U. 2006a. Food and feeding of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters after the 1997–98 El Niño event. Fish. Res. 79 16–27.

Markaida, U. 2006b. Population structure and reproductive biology of jumbo squid *Dosidicus gigas* from the Gulf of California after the 1997–1998 El Niño event. Fish. Res. 79 28–37.

Masuda, S., K. Yokawa, A. Yatsu, and S. Kawahara. 1998. Growth and Population Structure of *Dosidicus gigas* in the Southeastern Pacific Ocean. *In* Contributed papers to International Symposium on Large Pelagic Squids, July 18–19, 1996, T. Okutani, ed. Tokyo: Japan Marine Fishery Resources Research Center. 107–118 pp.

Morón, O., and M. Sarmiento. 1999. Detección de especies e invertebrados indicadores del fenómeno El Niño y otros trastornos con el medio ambiente. Callao, Perú: IMARPE.

Nesis, K. N. 1983. *Dosidicus gigas*. *In* Cephalpod Life Cycles. Volume I: Species Accounts, P. R. Boyle, ed. London: Academic Press. 475 pp.

Nigmatullin, C. M., K. N. Nesis, and A. I. Arkhipkin. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). Fish. Res. 54:9–19.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zelle. 2002. Towards sustainability in world fisheries. Nature 418:689–695.

Pauly, D., and M. L. Palomares. 2005. Fishing Down the Food Web: It Is Far More Pervasive Than We Thought. Bull. Mar. Sci. 76:197–211.

Pecl, G., and G. Jackson. 2006. Potential impacts of Climate Change on Loliginid Squid: Biology, Ecology & Fisheries. In: B. Olson and J. Young (Editors), The Role of Squid in Pelagic Marine Ecosystems—GLOBEC-CLIOTOP WG3 Workshop, University of Hawaii, Manoa.

Polis, G. A. 1981. The Evolution and Dynamics of Intraspecific Predation. Annu. Rev. Ecol. Syst. 12:225–251.

Rodhouse, P. G. 1998. Physiological Progenesis in Cephalopod Molluscs. Biol. Bull. 195:17–20.

Roper, C. F. E., M. J. Sweeney, and C. E. Nauen. 1984. Cephalopods of the World. FAO Fisheries Synopsis. 125 Vol. 3. Rome: FAO.

Sandoval-Castellanos, E., M. Uribe-Alcocer, and P. Díaz-Jaimes. 2007. Population genetic structure of jumbo squid (*Dosidicus gigas*) evaluated by RAPD analysis. Fish. Res. 83:113–118.

Shaffer, G., S. Hormazabal, O. Pizarro, and M. Ramos. 2004. Circulation and variability in the Chile Basin. Deep-Sea Res. I 51:1367–1386.

Staaf, D. J., S. Camarilla-Coop, S. H. D. Haddock, A. C. Nyack, J. Payne, C. A. Salinas-Zavala, B. A. Seibel, L. Trueblood, C. Widmer, and W. F. Gilly. 2008. Natural egg mass deposition by the Humboldt squid (*Dosidicus gigas*) in the Gulf of California and characteristics of hatchlings and paralarvae. J. Mar. Biol. Assoc. UK 88:759–770.

Tafur, R., P. Villegas, M. Rabí, and C. Yamashiro. 2001. Dynamics of maturation, seasonality of reproduction and spawning grounds of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in Peruvian waters. Fish. Res. 54:33–50.

Taipe, A., C. Yamashiro, L. Mariategui, P. Rojas, and C. Roque. 2001. Distribution and concentrations of jumbo flying squid (*Dosidicus gigas*) off the Peruvian coast between 1991 and 1999. Fish. Res. 54:21–32.

Tam, J., M. H. Taylor, V. Blasković, P. Espinoza, R. M. Ballón, E. Díaz, C. Wosnitza-Mendo, J. Argüelles, S. Purca, P. Ayón, L. Quipuzcoa, D. Gutiérrez, E. Goya, N. Ochoa, and M. Wolff. 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions. Prog. Oceanogr. DOI 10.1016/j.pocean. 2008.10.007

Taylor, M. H., J. Tam, V. Blasković, P. Espinoza, R. M. Ballón, C. Wosnitza-Mendo, J. Argüelles, E. Díaz, S. Purca, N. Ochoa, P. Ayón, E. Goya, D. Gutiérrez, L. Quipuzcoa, and M. Wolff. 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: Elucidating ecosystem dynamics from 1995-2004 with a focus on the impact of ENSO. Prog. Oceanogr. DOI 10.1016/j.pocean.2008.10.008.

Waluda, C. M., C. Yamashiro, C. D. Elvidge, V. R. Hobsond, and P. G. Rodhouse. 2004. Quantifying light-fishing for *Dosidicus gigas* in the eastern Pacific using satellite remote sensing. Remote Sens. Environ. 91:129–133.

Wolff, M., C. Wosnitza-Mendo, and J. Mendo. 2003. The Humboldt Current—Trends in exploitation, protection and research. *In* Large Marine Ecosystems of the World: Trends in exploitation, protection and research, G. Hempel and K. Sherman, eds. Amsterdam: Elsevier. 279–309 pp.

Yatsu, A., R. Tafur, and 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.

Zeidberg, L. D., and B. H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc. Natl. Acad. Sci. 104:12948–12950.