Extreme plasticity in life-history strategy allows a migratory predator (jumbo squid) to cope with a changing climate

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Abstract

Dosidicus gigas (jumbo or Humboldt squid) is a semelparous, major predator of the eastern Pacific that is ecologically and commercially important. In the Gulf of California, these animals mature at large size (>55 cm mantle length) in 1–1.5 years and have supported a major commercial fishery in the Guaymas Basin during the last 20 years. An El Niño event in 2009–2010, was accompanied by a collapse of this fishery, and squid in the region showed major changes in the distribution and life-history strategy. Large squid abandoned seasonal coastal-shelf habitats in 2010 and instead were found in the Salsipuedes Basin to the north, an area buffered from the effects of El Niño by tidal upwelling and a well-mixed water column. The commercial fishery also relocated to this region. Although large squid were not found in the Guaymas Basin from 2010 to 2012, small squid were abundant and matured at an unusually small mantle-length (<30 cm) and young age (approximately 6 months). Juvenile squid thus appeared to respond to El Niño with an alternative life-history trajectory in which gigantism and high fecundity in normally productive coastal-shelf habitats were traded for accelerated reproduction at small size in an offshore environment. Both small and large mature squid, were present in the Salsipuedes Basin during 2011, indicating that both life-history strategies can coexist. Hydro-acoustic data, reveal that squid biomass in this study area nearly doubled between 2010 and 2011, primarily due to a large increase in small squid that were not susceptible to the fishery. Such a climate-driven switch in size-at-maturity may allow D. gigas to rapidly adapt to and cope with El Niño. This ability is likely to be an important factor in conjunction with longerterm climate-change and the potential ecological impacts of this invasive predator on marine ecosystems.

Keywords: El Niño, jumbo squid, maturation, migration, range extension

Received 6 November 2012 and accepted 24 February 2013

Introduction

Understanding how ecologically and commercially important marine species cope with the environmental change is critical for evaluating the interacting effects of fisheries and climate change on marine ecosystem services (Harley et al., 2006; Doney et al., 2012). Many predatory fishes of commercial and ecological value are long-lived, and the necessity of long-term datasets to identify trends makes evaluating responses of a species to climate change challenging. Such datasets are still relatively rare. In contrast, responses of short-lived organisms, particularly invertebrates, to environmental change may be more readily quantified, but such species are generally not higher trophic level predators of great commercial importance. An exception to this generalization is provided by Dosidicus gigas (D’Orbigny 1835), commonly known as Humboldt or jumbo squid, a species that sustains the world’s largest invertebrate fishery (FAO, 2012) and is a major prey item for sperm whales and other marine mammals (Nigmatullin et al., 2001).
**Dosidicus gigas** is a large predator with a distribution in the eastern Pacific extending from Chile to Canada (Jereb & Roper, 2010). This squid can rapidly migrate long distances (Gilly et al., 2006a; Stewart et al., 2012) and has a flexible diet (Bazzino et al., 2007; Field et al., 2007; Markaida et al., 2008), high fecundity (Markaida & Sosa-Nishizaki, 2001), rapid growth rate and short-life span (Markaida et al., 2004). Taken together, these features suggest that *D. gigas* can respond rapidly, on both individual and population levels, to climatic changes as well as fishing pressure (Gilly & Markaida, 2007; Gilly et al., 2013). Such responses are likely to underlie the variable nature of the geographical distribution of the species, a feature that is particularly evident in episodic range extensions that occur at temperate latitudes in both hemispheres (Nesis, 1983; Nigmatullin et al., 2001). These range extensions can impact established food webs and fisheries (Caddy & Rodhouse, 1998; Field et al., 2007, 2012) as was reported for the Pacific hake fishery during the most recent range extension during the last decade (Zeidberg & Robison, 2007; Alarcón-Muñoz et al., 2008; Holmes et al., 2008).

In the Guaymas Basin of the Gulf of California, this squid typically matures at large size (>55 cm ML) in about 1 year, and large squid have historically accounted for commercial squid landings in Mexico (Markaida et al., 2004; Velazquez-Abunader et al., 2012). Coastal productivity, enhanced by wind-driven upwelling (Rodens & Groves, 1959; Moser et al., 1974; Thunell et al., 1996; Lluch-Cota, 2000; Kahrul et al., 2004), supports seasonal squid populations off the Baja California Peninsula in summer/fall and off the mainland state of Sonora in winter/spring (Markaida & Sosa-Nishizaki, 2001; Markaida et al., 2005). This pattern was disrupted following an El Niño event during winter of 2009–2010, and the fishery collapsed.

El Niño affects global weather patterns, oceanography, ecology, and economics (Yeh et al., 2009). In the eastern Pacific, El Niño leads to increased SST, a deeper thermocline, a reduction in primary production associated with wind-driven upwelling, and a variety of effects on higher trophic levels (Barber & Chavez, 1983; Sanchez-Velasco et al., 2002, 2004; Chavez et al., 2008, 2011; King et al., 2011). An adaptive response to El Niño might be expected for *Dosidicus gigas*, an eastern Pacific endemic well-known for opportunism (Gilly & Markaida, 2007).

This study analyzes the response of jumbo squid in the central Gulf of California to the 2009–2010 El Niño and subsequent La Niña, compares these changes to ones previously reported for other strong El Niños (1997–1998 and 1982–1983), and interprets these findings in a larger context relevant to this squid’s geographical range in the Northeast Pacific Ocean. Because of the importance of this species to oceanic food webs and fisheries, changes in abundance, distribution, diet, size, and reproductive strategy of jumbo squid have far-reaching ecological and economic consequences (Andre et al., 2010).

### Materials and methods

Studies were carried out between 2002 and 2011 in the central Gulf of California (Fig. 1 and Table S1). The Gulf is divided into two parts by a shallow sill (approximately 200 m depth) that separates the Salsipuedes Basin and the Guaymas Basin at approximately 28.5°N (white dashed curve in Fig. 1). In the Salsipuedes Basin, the water column is well mixed and productivity is driven by strong tidal currents and resultant upwelling. In contrast, the Guaymas Basin shares characteristics of the eastern Pacific Ocean and California Current, including primary productivity linked to coastal, wind-driven upwelling and a well-developed oxygen minimum zone (OMZ). Linkage to the Pacific Ocean also makes the southern half of the Gulf more susceptible to the influences of El Niño (Alvarez-Borrego & Lara-Lara, 1991; Bray & Robles, 1991). In this study, we focus on three areas within the greater Guaymas Basin – the open basin and traditional squid fishing areas on the Santa Rosalia and Guaymas shelves (Fig. 1).

Squid were sampled by jigging after dusk using weighted, luminous jigs (8–50 cm length). Stomachs were frozen, statoliths were stored in 70% ethanol or in dry paper, and reproductive tissue was fixed in 10% formalin. Assignment of sexual maturity stage was based on the visual criteria at the time of capture ([Lipinski & Underhill, 1995]; Stage I–II = immature, Stage III = maturing, Stage IV–V = mature).

### Aging

A statolith was attached to a glass slide using Crystalbond™ (Aremco Products Inc., Valley Cottage, NY, USA) with the wing and rostrum oriented upwards (Clarke, 1978; Lipinski, 1997). Gridding employed waterproof sandpaper (400, 1000 and 2000 grit). A ‘frontal’ sectioning plane (Lipinski & Durholtz, 1994) that passed through the dorsal dome to the nucleus avoided problems with occulted crystals across the dorsal dome (Arguelles et al., 2001). After a complete axis from the nucleus to dorsal dome was revealed, the Crystalbond was reheated, and the statolith was inverted and reattached. Gridding was resumed until the nucleus was visible. Final sections were covered with Canada balsam and a cover slip.

Mounted sections were viewed under a compound microscope (×400) and photographed. Overlapping images from the nucleus to the edge of the dorsal dome were assembled to create a complete transect, and increments were counted using ImageTool software (University of Texas Health Science Center, San Antonio, Texas). The total number of increments for each statolith was determined twice, and if the difference was >10%, a third count was made. The mean number of increments was taken to represent the age of the squid in days (Arkhipkin, 2004).
Fecundity

Three subsamples of ovaries (123 ± 43 µg of tissue; mean ± SD, n = 21) from seven squid were analyzed. Oocytes were torn off the ovarian blood vessels in a Bogorov chamber using forceps and a dissection pin, and all oocytes were counted under a stereomicroscope. Mean oocyte density (oocytes µg⁻¹) was 287.3 ± 4.7, n = 21). The number of counted oocytes in the three subsamples was extrapolated to the total weight of the ovary for that squid to yield the total number of ovarian oocytes. The number of ova in the oviduct, was estimated in a similar manner from the number of ova in a single subsample of oviduct (mean density (ova µg⁻¹) = 2.4 ± 0.3; n = 7) and scaling to the weight of the oviduct for that squid. Potential fecundity was calculated as the sum of oocytes in the ovary and ova in the oviduct.

Diet

Stomachs were thawed in seawater, and the contents were sieved and prepared as described elsewhere (Markaida & Sosa-Nishizaki, 2003). Prey items were visually identified under a stereomicroscope by undigested hard parts, enumerated and assigned to the finest taxonomic level possible. Frequency of occurrence (%FO) and the number (%N) were used to quantify the diet (Markaida, 2006a; Markaida et al., 2008).
Water-column properties

Temperature-at-depth profiles were recorded in 2009–2012 during January through April in the southern Gulf of California (numbered areas in Fig. 1, Table S2). A conventional profiler (SBE19plusv2; Seabird Electronics, Bellevue, WA, USA) was deployed from the National Geographic Sea Bird vessel operated by Lindblad Expeditions (New York, NY) (data in Fig. S1).

Remote sensing

For the period 2009–2011, Level-3 seasonal composites of surface Chlorophyll a (Chl a) concentration and sea-surface temperature (SST) at 4.6 km resolution, as well as seasonal climatology for both parameters (2002-present), were derived from the MODerate resolution Imaging Spectroradiometer (MODIS; http://oceancolor.gsfc.nasa.gov/). All images were projected onto an equal-area grid of the Gulf of California, and produced seasonal anomaly maps were produced by subtracting the appropriate seasonal climatology from individual seasonal images (Figs S2 and S3).

For time-series analysis (Fig. 2), Chl a data from both the Sea-viewing Wide Field-of-view Sensor (SeaWiFS; 1997–2004) and MODIS (2005–2011) were used. These sensors utilize different spectral bands and give slightly different values for Chl a; however, anomalies should be less affected by this issue than absolute values. For both sensors, Chl a anomaly

![Fig. 2](image)

Fig. 2 Time course of sea-surface temperature (SST) and Chl a anomalies from 1997 to 2012. Areas for remote-sensing analysis are indicated in Fig. 1. Boxed areas indicate the 2009–2010 El Niño–note similarities to the 1997–1998 event. (a) Open Guaymas Basin. (b) Guaymas coastal shelf. (c) Santa Rosalia coastal shelf. (d) Salsipuedes Basin. (e) Time course of Chl a concentrations from 2009 to 2011. Chl a in the open Guaymas Basin (black trace) is generally much lower than on the coastal shelves, but the area is still reasonably productive except in summer, when Chl a is at a minimum in all areas. SST and Chl a time-series data were smoothed using a 15-day rolling mean.
The time-series were generated using 8-day composites that were compared with climatological values over the entire record of each respective sensor. Daily SST data for the time-series analysis were derived from the Reynolds Optimum Interpolation SST (OISST) Version 2 product (Reynolds et al. 2002) from the Advanced Very High Resolution Radiometer at 0.25° resolution, obtained from NOAA.

All Chl a data were generated from the standard empirical global algorithms employing the most recent reprocessing. Satellite imagery was processed using NASA’s SeaWiFS Data Analysis System (SeaDAS) Version 6.3 (http://seadas.gsfc.nasa.gov/).

**Hydro-acoustics**

Data were collected with calibrated, split-beam, multi-frequency echosounders (Simrad, EK60) as described elsewhere (Benoit-Bird & Gilly, 2012). Squid were identified in the acoustic data based on the frequency response of both individually localized targets and volume scattering. After classification, volume scattering and 38 kHz target strength over the upper 500 m of the water column were averaged in 1 km bins. Target strength was converted to mean (squid) length, and volume scattering to total biomass, using the relationships established from experimental work (Benoit-Bird et al., 2008; Benoit-Bird, unpublished data). The biomass density estimate (kg km⁻²) was then multiplied by the total area represented by each transect (transect length multiplied by half the distance to the next nearest transect), and those estimates were summed to create an estimate of squid biomass in each study region.

**Results**

**Effects of El Niño on water-column properties and chlorophyll a**

An intense El Niño, arguably the strongest since the 1997–1998 event (Barnard et al., 2011; http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml; http://ggweather.com/enso/oni.htm), occurred from July 2009 through April 2010 and affected the upper water column in the southern Gulf of California during this period (Fig. S1). Isotherms between 15 °C and 20 °C from Cabo San Lucas to Santa Rosalia were significantly depressed during the winter of 2010 (Fig. S1b) and recovered by winter 2011 (Fig. S1c) SST was also clearly abnormally warm during this period (Fig. S2).

Depression of the thermocline during El Niño is associated with decreased primary production in wind-driven upwelling systems in the eastern Pacific Ocean due to nutrient-poor warm water in the upper water column (Barber & Chavez, 1983; Chavez et al., 2011), and such an effect is evident in the Chl a anomaly during winter-spring of 2010 in the southern Gulf along the Sonora coast (south of approximately 26.5°N) and the Pacific coast of the Baja California Peninsula (Fig. S3). Effects on Chl a levels in the Guaymas Basin were weaker and more variable. Time-series of SST and Chl a anomalies for our study areas (Fig. 2) reveal a small positive Chl a anomaly over the open basin (Fig. 2a) during the 2009–2010 El Niño and a much stronger negative anomaly on the Guaymas shelf, as was observed during the 1997–1998 El Niño (Fig. 2b). The Santa Rosalia shelf showed a mixed pattern with a biphasic anomaly (Fig. 2c). During the subsequent cold La Niña period, Chl a anomalies for the shelf regions were much more positive than over the open basin. Thus, the open basin is generally less productive than the coastal shelves, but it is more stable over time (Fig. 2e).

**Collapse of the Guaymas Basin squid fishery and relocation to the Salsipuedes Basin**

Commercial squid landings in the Gulf of California have been almost entirely from the Santa Rosalia and Guaymas shelf areas since the current large-scale fishery began in 1994. Landings fluctuated between 50 000 and 110 000 tons between 1995 and 2009 (mean ± SD = 70 142 ± 21 137) (Fig. 3), with the exception of 1998 (8900 tons) due to the 1997–1998 El Niño (Morales-Bojorquez et al., 2001). In 2009–2010, this fishery collapsed due to the lack of squid on the established fishing grounds, and large commercial landings were reported from the Salsipuedes Basin (landings in Bahía de Los Ángeles) for the first time. This region appeared to be minimally affected by the 2009–2010 El Niño, as evidenced by the relatively small SST anomaly and the absence of a negative Chl a anomaly during the event (Fig. 2d, Fig. S3). Chlorophyll a, an indicator of primary productivity, remained relatively high throughout 2011, and this area is generally productive throughout much of the year (Fig. 2e).

Hydro-acoustic surveys revealed that biomass of squid in our survey region within the greater Guaymas Basin was high both before and after El Niño (64 000–91 000 tons; see Table 1). Individual subareas within the Guaymas Basin varied from year to year, probably reflecting seasonal changes in local abundance, which is also characteristic of the squid fishery. Our sampling regime covered the major fishing areas and the area connecting them. Because squid migrate from one shelf to the other across the open basin (Markaida et al., 2005; Gilly et al., 2006a), our estimates of total biomass for the greater Guaymas Basin should not be critically dependent on the time of year that sampling was carried out. Although we do not have acoustic data from the Salsipuedes Basin prior to 2010, it is clear that biomass of squid in this area increased dramatically.
between June 2010 and June 2011. Thus, total squid biomass in the Guaymas Basin and Salsipuedes Basin may have increased following El Niño. Most of these squid were too small to be effectively harvested with existing commercial fishing methods, and therefore landings greatly declined despite an apparently increased stock size.

**Size and maturity of squid before and after El Niño**

All squid sampled by jigging in Guaymas Basin (south of 28.3°N) in 2010 (GB10, Fig. 4a) and 2011 (GB11, Fig. 4b) including the traditional Santa Rosalia fishing grounds, were unusually small (<40 cm ML) in comparison to the vast majority of squid sampled from the Santa Rosalia (SR08, Fig. 4c) or Guaymas (G02, Table S1, ML = 56.7 ± 7.6 cm, n = 997) fishing grounds in previous years (see also Nevárez-Martínez et al., 2006; Nevárez-Martínez et al., 2010). Small squid (<50 cm ML) in the SR08 sample were all immature (open bars in Fig. 4c) and obviously outliers, but many small squid in 2010 (37 of 122) and 2011 (147 of 281) were mature (stage IV or V, filled bars in Figs 4a and b). This highly unusual pattern has persisted; 44 squid from Santa Rosalia sampled in Sept. 2012 were all small (<40 cm ML), and 36 were mature (SR12, Table 2). A radical shift in size-at-maturity thus occurred in the Guaymas Basin after the 2009–2010 Niño and has persisted through 2012 (Fig. 4f).

Both large (>50 cm ML) and small (<50 cm ML) squid, were sampled in the Salsipuedes Basin in 2010 (SB10, Fig. 4e) and 2011 (SB11, Fig. 4f). Most large squid in this region were mature in both years (filled bars in Figs 4d and e). Small squid were all immature in 2010 (Fig. 4d), but small mature squid were clearly present in 2011 (Fig. 4e and f). The lack of small mature squid in 2010 may simply be due to the small sample size, but the small size of these squid indicates that they are not of the same cohort as the larger animals. Thus,

### Table 1 Biomass and median lengths of *Dosidicus gigas* estimated using active acoustics. Locations are indicated in Fig. 1. The Greater Guaymas Basin entries are the sum of the three subareas within the basin. Very low estimates of biomass in all regions in Feb. 2011 were made during the same period that the commercial squid fishing fleet could not locate large densities of squid in the region mapped in Fig. 1. It is unlikely that the total biomass decreased to this extent, and presumably squid transiently migrated out of the areas surveyed.

<table>
<thead>
<tr>
<th>Location</th>
<th>Total biomass in metric tonn (median length in cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Santa Rosalia Shelf</td>
<td>73 000 (70)</td>
</tr>
<tr>
<td>Guaymas Shelf</td>
<td>13 000 (42)</td>
</tr>
<tr>
<td>Open Guaymas Basin</td>
<td>5000 (52)</td>
</tr>
<tr>
<td>Greater Guaymas Basin</td>
<td>91 000</td>
</tr>
<tr>
<td>Salsipuedes Basin</td>
<td>6000 (45)</td>
</tr>
</tbody>
</table>
unlike the situation in the Guaymas Basin, two sizes-at-maturity were evident in 2011 (and probably also in 2010). We do not have data from this area in 2012.

**Diet of squid before and after El Niño**

Stomach-content analysis of the small squid in the open Guaymas Basin in 2010 revealed a diverse mixture of mesopelagic micronekton, particularly myctophids, squid and pteropods, but also a major contribution from crustaceans (Fig. S4a). A similarly diverse diet was evident on the Santa Rosalia shelf, but the contribution by euphausiids here was much greater (Fig. S4b). The diet of squid in the greater Guaymas Basin in 2011 (Figs S4e and f) was composed primarily of micronekton, again with a significant proportion of euphausiids. Except for the prevalence of crustaceans, this diet is typical for this area based on sampling during 2005–2007 (Fig. S4h) and in earlier years (Markaida & Sosa-Nishizaki, 2003; Markaida et al., 2008). Squid in the Salsipuedes Basin had a drastically different diet in 2010. Small squid in this area foraged primarily on anchovy, and euphausiids represented the only mesopelagic prey (Fig. S4c). Large squid consumed mostly euphausiids, but also an assortment of fish, including some myctophids (Fig. S4d). Consumption of myctophids by small squid (33–47 cm ML) in this region was also found in 2011 along with a very high proportion of anchovy (Fig. S4g). Consumption of euphausiids appeared to be much less than in 2010, but we do not have diet data for large squid here in 2011 for comparison. The relatively minor amount of mesopelagic micronekton (other than euphausiids) in the diet of squid here stands in qualitative contrast to the picture in the greater Guaymas Basin, both before and after El Niño.

Measurements of water-column properties confirmed a well-developed OMZ (oxygen concentration of <20 μmol kg⁻¹) throughout the Guaymas Basin and an
absence of this feature in the Salsipuedes Basin (data not illustrated; see Alvarez-Borrego & Lara-Lara, 1991; Gilly et al., 2012). Squid in the Salsipuedes Basin thus inhabit a different mesopelagic environment than those in the Guaymas Basin, and the difference in consumption of myctophids and other mesopelagic micronekton presumably reflects the large differences between these two midwater ecosystems and not the size of the squid. Dietary adaptability of jumbo squid in invading new environments has previously been documented, and dietary adjustment here is consistent with this idea (Field et al., 2007, 2012; Stewart et al., 2012).

_Fecundity of small vs. large mature squid_

Potential fecundity was determined for small mature squid from the Guaymas Basin in 2011 (Fig. S5). Fecundity increases exponentially with mantle length, with small squid (mean ML = 35.4 ± 7.2 cm) having an average of 0.8 ± 0.6 × 10^6 oocytes ($n = 7$) vs. 18.7 ± 7.3 × 10^6 ($n = 11$) for large squid (mean ML = 74.0 ± 7.32 cm) based on published data from the same region in earlier years (Nigmatullin & Markaida, 2009). Reproductive output is thus vastly reduced at the individual level for the smaller post-El Niño squid.

_Differences in size and age of mature squid over time and space_

Statoliths were aged for 37 small squid from the greater Guaymas Basin in June 2010 and 2011, and the youngest age for a mature squid corresponded to 146 increments in 2010 and 216 in 2011 (GB10 and GB11, Table 2). Squid sampled in September 2010 were of similar age and size (GB10B, Table 2). Large squid previously sampled in Santa Rosalia (June 2005) were of much greater age at maturity (324–430 increments; Table 2). Squid in the Guaymas Basin thus matured at an unusually small size in approximately 6 months after El Niño.

When viewed more broadly over the geographical range of _D. gigas_, it is clear that the size and age at maturity vary widely and proportionately. The smallest mature squid we sampled (solid circles in Fig. 5) were those from the Guaymas Basin immediately after the 2009–2010 El Niño (June 2010, GB10), and the largest (and oldest) mature squid in Mexico were from Magdalena Bay on the Pacific coast of the Baja Peninsula in 2005 (MB05, Fig. 5). Squid from Santa Rosalia in 2005 (SR05) and in the Pacific Ocean off central California in 2009 (NP09, Table 2) were comparable. The largest squid (approximately 470 days old) in our collection were from coastal Chile in 2005 (Chile05). In nearly all samples, the mean ages (and sizes) for immature squid were within 10% of the mature values, suggesting that maturation occurs rapidly regardless of size.

Additional data for mature squid captured in the Chinese commercial fishery for _D. gigas_ outside the EEZs of Costa Rica, Peru, and Chile are plotted in Fig. 5 (open symbols). Values from Costa Rica (circle) are similar to our values for GB samples and ETP06 (Table 2). Squid from Peru (squares and triangles) cluster into two groups, one extremely large (>90 cm ML) and one much smaller (35–50 cm ML). Mature Chilean squid

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**Table 2** Aging and size data for mature squid. Sample codes are identified in Table 1; total in parentheses indicates number of statoliths aged form mature squid. First age is age of the youngest mature specimen in the sample; Male and Female Ages are means ± SD

<table>
<thead>
<tr>
<th>Sample (n)</th>
<th>First age (rings)</th>
<th>ML (cm)</th>
<th>Age (rings)</th>
<th>Weight (kg)</th>
<th>Male ML (n)</th>
<th>Male age (rings)</th>
<th>Female ML (n)</th>
<th>Female age (rings)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GB10 (5)</td>
<td>146</td>
<td>21.8±3.6</td>
<td>183±26.4</td>
<td>0.6±0.3</td>
<td>25.3±5.4 (3)</td>
<td>178±33.2</td>
<td>33.0 (2)</td>
<td>190</td>
</tr>
<tr>
<td>GB10B (3)</td>
<td>217</td>
<td>38.5±2.6</td>
<td>226±10.8</td>
<td>2.0</td>
<td>38.5±2.7 (3)</td>
<td>226±10.8</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>GB11 (22)</td>
<td>216</td>
<td>37.3±3.9</td>
<td>254±26.6</td>
<td>1.2±0.5</td>
<td>35.1±2.2 (4)</td>
<td>246±21.4</td>
<td>38±4.1 (18)</td>
<td>256±27.9</td>
</tr>
<tr>
<td>SB10 (1)</td>
<td>238</td>
<td>55</td>
<td>238</td>
<td>4.1</td>
<td>–</td>
<td>–</td>
<td>55.0 (1)</td>
<td>238</td>
</tr>
<tr>
<td>SR05 (3)</td>
<td>324</td>
<td>60.7±5.1</td>
<td>366±56.4</td>
<td>–</td>
<td>60.7±5.1 (3)</td>
<td>366±56.4</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>MB05 (19)</td>
<td>321</td>
<td>73.8±2.9</td>
<td>405±58.6</td>
<td>–</td>
<td>71.2±2.8 (7)</td>
<td>399±35.8</td>
<td>75.4±1.7 (12)</td>
<td>408±69.8</td>
</tr>
<tr>
<td>NP09 (1)</td>
<td>337</td>
<td>67</td>
<td>337</td>
<td>–</td>
<td>67 (1)</td>
<td>–</td>
<td>337</td>
<td>–</td>
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<tr>
<td>ETP06 (2)</td>
<td>213</td>
<td>33</td>
<td>229.5</td>
<td>–</td>
<td>33 (2)</td>
<td>–</td>
<td>229.5</td>
<td>–</td>
</tr>
<tr>
<td>Chile05 (6)</td>
<td>394</td>
<td>84.7±4.3</td>
<td>474±67.4</td>
<td>19.7±3.1</td>
<td>85.9±3.9 (5)</td>
<td>476±76.4</td>
<td>80 (1)</td>
<td>464</td>
</tr>
<tr>
<td>GB07 (17)</td>
<td>–</td>
<td>62.2±7.7</td>
<td>–</td>
<td>9.7±3.3</td>
<td>58.3±6.6 (11)</td>
<td>–</td>
<td>69.2±3.9 (6)</td>
<td>–</td>
</tr>
<tr>
<td>FB08*</td>
<td>–</td>
<td>77.7±6.2</td>
<td>–</td>
<td>–</td>
<td>62 (1)</td>
<td>–</td>
<td>79.4±3.0 (9)</td>
<td>–</td>
</tr>
<tr>
<td>&gt;62 cm (10)</td>
<td>–</td>
<td>37.4±3.2</td>
<td>–</td>
<td>–</td>
<td>36.8±3.5 (3)</td>
<td>–</td>
<td>37.4±3.2 (51)</td>
<td>–</td>
</tr>
<tr>
<td>&lt;44 cm (54)</td>
<td>–</td>
<td>28.6±4.7</td>
<td>–</td>
<td>0.6±0.3</td>
<td>33.7±5.5 (3)</td>
<td>–</td>
<td>28.1±4.4 (33)</td>
<td>–</td>
</tr>
<tr>
<td>SR12 (36)</td>
<td>–</td>
<td>64.2±8.6</td>
<td>–</td>
<td>7.2±4.4</td>
<td>62.3±7.0 (50)</td>
<td>–</td>
<td>77.8±7.0 (7)</td>
<td>–</td>
</tr>
</tbody>
</table>

*FB08 was divided into two groups of different ML.
were approximately 40 cm ML (hexagon). All of these samples are in reasonable agreement with a linear relationship between ML and age.

Discussion

A large decrease in size-at-maturity, longevity, and fecundity of jumbo squid (Dosidicus gigas) in the Gulf of California occurred during the winter of 2009–2010. The timing of this transformation coincided with a strong El Niño event, but these changes have persisted through multiple generations of squid to the present time. We propose that this adjustable life-history strategy, revealed by an acute response to El Niño, is an important factor in the ability of this ecologically and economically important squid to adapt to slower forms of climate change.

Response of jumbo squid in the Guaymas Basin to the 2009–2010 El Niño

Commercial squid fishing in the Guaymas Basin crashed in 2010 after El Niño (Fig. 3). This fishery normally targets large squid that are seasonally present in high abundance on the coastal shelf areas off Santa Rosalia and Guaymas. Although we captured large squid near Santa Rosalia in September 2009 (Gilly et al., 2012), we failed to capture large squid anywhere in the Guaymas Basin after El Niño (June 2010) or during the subsequent La Niña (February and June 2011). We propose that jumbo squid reacted to El Niño by abandoning the favored coastal shelf regions sometime during the fall of 2009 when El Niño was reaching its peak and altering their life-history strategy in one of two ways.

In one case, some squid appeared to migrate north to the Salsipuedes Basin because large, mature squid were present there in commercial quantities in June 2010 for the first time. Based on the ML-age relation in Fig. 5, these squid (>55 cm ML; Fig. 4d) were approximately 300 days old (see also SB10, Table 2), so they would have been born in late summer of 2009 as El Niño was intensifying. These squid would therefore have had a ML of approximately 30 cm during spring 2010 when a strong effect of El Niño on the upper water column in the Guaymas Basin was apparent (Fig. S1). Migration to the Salsipuedes Basin around this time may have allowed maturity to progress ‘normally’ with a 1-year life-span to large size, consistent with the fact that productivity here depends on tidal upwelling (Parker, 1964), which can provide a buffer from the impacts of El Niño felt further south (Tershy et al., 1991; Sanchez-Velaso et al., 2000). Our remote-sensing data are consistent with this idea (Fig. 2d).

In another strategy, squid remained resident in the open Guaymas Basin. Small mature squid in the Guaymas Basin in June 2010 were approximately 150 days old and would therefore have been born in winter of 2010 (Table 2 and Fig. 5). We propose that the parents of these squid were also born in summer 2009 as El Niño developed, but this cohort did not emigrate and remained in the blue-water (and thermally altered) environment of the open Guaymas Basin. Productivity here is lower than on the coastal shelves (Fig. 2e), but appears to be less impacted by El Niño (Fig. 2d). This habitat choice must be tightly coupled to precocious maturation, as no large squid whatsoever were found in the Guaymas Basin at a time (June 2010) when they would be expected to be present in large numbers.

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based on a decade of previous work (Markaida et al., 2005; and unpublished data).

Both of the above patterns in squid distribution persisted during the 2011 La Niña, but both small and large mature squid were present in the Salsipuedes Basin in June 2011. This indicates that local physical and biological factors of the environment inhabited by adult squid cannot completely account for the simultaneous existence of the two reproductive strategies.

Comparison to the 1997-98 El Niño

Several important features of the response of jumbo squid to the 2009–2010 El Niño appear to have occurred in conjunction with the 1997–1998 event. First, large squid disappeared from the Guaymas Basin after the 1997–98 El Niño resulting in the fishery collapse in 1998 (Fig. 3), and large squid were only reported in the Gulf between 27.5 and 28.5°N (Nevárez-Martínez et al., 2002; an area that includes the Salsipuedes Basin. Sperm whales also changed their distribution by dispersing from established aggregation areas in the Guaymas Basin, presumably because their squid prey had relocated (Jaquet & Gendron, 2002), but they appeared to remain within the Gulf of California (Ruiz-Cooley et al. 2004). Second, a dramatic decrease in ML (50–75%) for mature squid occurred in the Santa Rosalia region in 1998–1999 compared to years before and after this period (Nevárez-Martínez et al., 2006; Bazzino et al., 2007). Return to a large size-at-maturity took several years (Markaida, 2006a), with large squid returning to the Gulf by 2000 (Morales-Bojorquez & Nevarez-Martínez, 2010). Third, the diet of squid in the Guaymas Basin did not drastically change, but crustaceans were a much more prominent dietary component in 1999 than in years before El Niño (Markaida, 2006b). Fourth, large squid were caught in 1999 on the Pacific coast of the Baja California peninsula in unusually large quantities (Fig. 3). This increase was suggested to result from emigration of squid from the Gulf of California (Morales-Bojorquez et al., 2001), but there is no direct evidence for such a migration. Parallels in this suite of results between 1997–1998 and 2009–2010 make it extremely likely that a strong El Niño was the driver of these changes in each case. Other periods of moderately warm SST anomaly occurred between 1998 and 2010, but none of these periods was classified as a strong El Niño or led to comparable ecological changes.

Changes in jumbo squid distribution beyond the Guaymas Basin

Jumbo squid essentially disappeared from the Pacific coast of the USA and Canada in early 2010 through most of 2012 (Bjorkstedt et al., 2011; Stewart, 2012). Although the 2009–2010 El Niño did not significantly alter SST in this northern region, a midwater temperature anomaly (up to +2 °C at 100 m depth) occurred during January–March 2010 (http://www.mbari.org/bog/Projects/MOOS/M1.html). This anomaly is associated with poleward propagation of Kelvin waves driven by the El Niño Southern Oscillation (S. Bograd, NOAA, personal communication), and the 2010 signal at 100 m depth in Monterey was stronger than any since 1998. We hypothesize that the D. gigas population off the northeast Pacific coast in 2010 moved offshore from the coastal shelf area, possibly beyond the California Current in a response analogous to that that shown by squid in the Guaymas Basin at the same time.

The 1997–98 El Niño marked the beginning of a major range extension of D. gigas that occurred over the next decade (Zeidberg & Robison, 2007) and lasted until the perturbation provided by the 2009–2010 event. We hypothesize that the earlier invasion and subsequent northward expansion are analogous to the situation for the Salsipuedes Basin and the 2009–2010 El Niño. The future of the squid population in Monterey Bay or the Salsipuedes Basin remains uncertain, but large numbers of small (<40 cm ML) maturing D. gigas have recently appeared off the California coast from Santa Cruz to San Diego (unpublished data; http://www.utsandiego.com/news/2013/jan/06/giant-squid-invade-san-diego-waters/). Only the future will reveal whether these formerly colonized areas will again support a large population of D. gigas and what size mature animals will attain.

Costs and benefits for maturing at small size

Plasticity in life-history characteristics and associated trade-offs (Mangel & Stamps, 2001) are well known in both squids (Boyle & Boletzky, 1996; Arkhipkin, 2004; Pecl & Jackson, 2008) and a variety of fishes, including sardine and anchovy (MacCall, 2009) and salmonids (Thorpe, 2007; Vincenzi et al., 2012). In these and other examples, large body size is typically positively correlated with a number of fitness traits, including higher fecundity, such that body size is frequently used as a proxy for fitness (Dmitriew, 2011). Squid grow larger with an adequate food supply and tend to live longer, resulting in large body sizes and extremely high fecundity after approximately 1 year. If a productive environment can support gigantism, there are advantages, including access to larger prey (Field et al., 2012), greatly increased reproductive output and probably a reduced risk of mortality due to predation (O’Dor, 1998).

In an environment that cannot sustain a large population of big squid, because of food limitations, an
individual squid never gets large and reproduces at a small size and young age. This is the case in the ETP and Costa Rica Dome (Fig. 5 and (Nigmatullin et al., 2001)), and warmer temperatures in the upper water column on a year-round basis are likely also an important factor. Maturing at a small size would be beneficial as the cumulative probability of predation before reaching maturity would be reduced, and the shorter life cycle would permit rapid population turn-over and growth. These features would also facilitate colonization of new areas, particularly in conjunction with migrations driven by an El Niño response. This is consistent with the increased biomass of D. gigas in our study area following El Niño (Table 1).

**Flexibility in size-at-maturity**

The response to El Niño by D. gigas in the Guaymas Basin clearly indicates that there are alternative reproductive strategies that give rise to mature animals with greatly different size-at-maturity characteristics and that both strategies can coexist. In addition, individuals can mature over a wide range of proportional MLs, depending on where and when a population was sampled (Fig. 5).

Discrete size-at-maturity groups of D. gigas that may represent genetically distinct populations have often been associated with equatorial ('small,' 13–34 cm ML) vs. higher-latitude ('large,' >50 cm ML) waters, with a third ‘medium’-sized group being found over most of the species range (24–60 cm ML (Nigmatullin et al., 2001). This concept has been questioned, with differences in size-at-maturity in the Peru Current System being associated with phenotypic plasticity coupled to environmental changes, primarily thorough movements of large-scale water masses driven by La Niña/El Niño events (Arguelles et al., 2008; Keyl et al., 2008, 2011; Tafur et al., 2010). In addition, genetic data do not support significant population structure for D. gigas based on body size or geography (Sandoval-Castellanos et al., 2010; Staaf et al., 2010; Ibáñez et al., 2011).

We propose that spatial (and temporal) heterogeneity in productivity and a complex dynamic between growth and sustainable foraging leads to a size-at-maturity that is unique for every population of D. gigas. In permanently warm tropical waters of modest productivity, squid mature at small size and young age; in temperate waters of seasonally high productivity, they can live longer and grow larger. Precisely what factors set the age at which maturation occurs in an individual squid or in a given population remain unknown, but this pattern is consistent with latitudinal trends in body size and longevity in other taxa (Blackburn et al., 1999; Munch & Salinas, 2009).

This growth-foraging-maturation dynamic would be expected to be sensitive to environmental conditions, both physical and biological. In this view, El Niño is an extreme driver that can push most or all of a temperate population of large squid to mature at a size (and age) comparable to that seen in the ETP. Other drivers undoubtedly exist that operate on a variety of spatial and temporal scales. Local or regional groups of squid may experience different suites of drivers, yet come to coexist at some time and place, with more than one size-at-maturity class being evident. This situation has not been reported in the Guaymas Basin, but it clearly occurred in the Salsipuedes Basin in 2011 (Fig. 4f), in the Farallon Basin in 2008 (Table 2) and in Peruvian waters in 2009 (open squares in Fig. 5) and 1992 (Tafur et al., 2001).

We propose that D. gigas is capable of maturing at any ML > 20–30 cm, but regional productivity tends to be either low or high, resulting in a correspondingly smaller or larger size-at-maturity. As part of this view, the post-El Niño squid found in Guaymas Basin represent a ‘minimal’ size-at-maturity condition that can give rise to populations of individuals that live for varying amounts of time and reach a corresponding age and size at maturity. Size and age of each population is ultimately determined by the conditions of a specific area at any given time. In some cases, particularly when environmental unpredictability may be involved, both small and large size-at-maturity animals can coexist.

**What controls changes in size-at-maturity?**

Population dynamics of squid are in part driven by phenotypic plasticity in response to environmental change (Boyle & Boletzky, 1996), and significant intraspecific differences in growth and size-at-maturity can become established between different populations (Pecl & Jackson, 2008; Ichii et al., 2009). Elevated temperatures and limited nutrition typically result in smaller size at maturity for squid (Boucher-Rodoni, 1973; Rowe & Mangold, 1975; Mangold, 1987; Forsythe & Hanlon, 1989; Arkhipkin & Mikheev, 1992; Jackson, 1995; Jackson & Domeier, 2003; Moreno et al., 2005).

This generalization regarding temperature is consistent with the smaller size of mature squid that would have been born in the Guaymas Basin during the 2009–2010 El Niño. Water temperatures over the upper 100 m were unusually warm during this period (Fig. S1), and SST was elevated over the greater Guaymas Basin (Fig. 2 and Fig. S2).

Nutritional factors are more difficult to evaluate. Strong El Niños can decrease primary productivity and exert downstream impacts on higher trophic levels.
Such effects could lead to a reduction in prey for maturing squid during and after El Niño, but previous strong El Niños have not produced such changes in the Gulf of California (unlike the Peru and California Current Systems – see Introduction). Neither primary (Santamariadelangel et al., 1994) or secondary (Jimenez-Perez & Lara-Lara, 1988) productivity, nor euphausiid abundance (Lavanigos-Espejo et al., 1989) were greatly affected by the strong 1982–1983 El Niño event, although some changes in species composition were noted. Myctophid larvae were reported to be more abundant in the central Gulf of California during the 1997–98 El Niño than during the subsequent La Niña (Valos-Garcia et al., 2003; Sanchez-Velasco et al., 2004). Although the possibility of chronically decreased nutrition cannot be ruled out, the persistence of small size-at-maturity squid throughout 2010–2012 makes this seem less likely.

Primary productivity (as judged by Chl a) decreased on the Santa Rosalia and Guaymas shelves, the traditional squid-fishing areas that were abandoned by large squid by the end of El Niño (June 2010). Negative Chl a anomalies were absent in both the open Guaymas Basin and Salsipuedes Basin, and these areas became the favored habitat for squid after El Niño. There is thus a correlation between decreased primary productivity on shelf habitats during El Niño and the tendency for large squid to abandon such areas and to relocate to areas that did not show such a strong productivity decrease. Major negative Chl a anomalies also occurred on the Guaymas and Santa Rosalia shelves in 2007 and 2008, respectively (Figs 2b and c), but neither was associated with a major positive SST anomaly or obvious disruption of the squid fishery (Fig. 3). Thus, primary productivity would seem to be a critical factor to squid distribution only through an association with strong El Niño conditions.

Pelagic egg masses of D. gigas appear to be deposited in the open Guaymas Basin at a pycnocline depth of approximately 20 m (Staaf et al., 2008) over a broad temperature range of 17–30 °C (Gilly et al., 2006b; Camarillo-Coop et al., 2011; Staaf et al., 2011). Eggs deposited during El Niño and developing juvenile squid would have been exposed to an anomalous thermal gradient in the upper 100 m (Fig. S1). Exposure to this physical anomaly may have led to altered biochemical pathways coupled to gene expression networks that control growth and maturation, thereby providing a switching mechanism for fixing the reaction pathway to El Niño relatively early in life, resulting in a small, early maturing phenotype.

Sudden transformation of a generation of squid by such a mechanism is plausible, but it cannot account for the long persistence of small size-at-maturity, despite the apparent return of relevant environmental factors to normal. The small, early-maturing phenotype appears to have decoupled from the environmental influences that previously supported gigantism on the Santa Rosalia and Guaymas shelves, and such a persistent transformation could be controlled by an epigenetic mechanism (Richards, 2006; Angers et al., 2010; Moran & Perez-Figueroa, 2011) that might lead to rapid appearance of an adaptive phenotype with transmission to subsequent generations (Rando & Verstrepen, 2007; Llamas et al., 2012). These features of epigenetic modification and inheritance are consistent with our observations, but we acknowledge the speculative nature of this hypothesis.

Coping with slower forms of climate change

Dosidicus gigas can drastically alter its life-history strategy in response to El Niño, a discrete and reasonably well understood environmental perturbation that is a prominent feature of the eastern Pacific Ocean. This ability is also likely to allow D. gigas to cope with slower forms of climate change, including natural multidecadal oscillations and long-term warming. Tolerance of temperature and oxygen extremes, a highly flexible diet, rapid growth rate and the ability to rapidly migrate long distances have been previously suggested to define a suite of characters underlying the recent range extension by D. gigas in relation to environmental change, particularly shoaling of the OMZ (Gilly & Markaida, 2007; Stewart et al., 2012; Gilly et al., 2013). We can now add the ability to radically alter the life-history trajectory, allowing the squid under some circumstances to attain large size and succeed as a major top predator—and under others to take on a much smaller, more rapidly reproducing phenotype that may readily expand into new areas.

Interactions between El Niño and slower forms of climate changes are likely but not well understood, particularly in regard to different types of El Niño (Yeh et al., 2009; Boucharel et al., 2011; Jung et al., 2011). The 2009–2010 event has been associated with the Central Pacific variant (El Niño Modoki) that is predicted to increase in frequency with global warming (Yeh et al., 2009; Barnard et al., 2011). If so, continuing changes in distribution and characteristics of D. gigas may provide a valuable indication of ongoing oceanic climate change and yield insight into the ecological impacts of climate change in the broadest sense. Indeed, a period of warming and reduced upwelling in the Guaymas Basin since 2004 has been associated with a concomitant decrease in commercial squid landings in this region (Robinson et al., 2012).

A possible outcome of the combination of increased El Niño activity, global warming and shoaling of OMZs...
could be the quasipermanent transformation of the D. gigas phenotype in a given temperate region such as the Gulf of California, a moderately warming Large Marine Ecosystem (Belkin, 2009), or Monterey Bay to the minimal size-at-maturity form and push the geographical boundary for the alternate jumbo form to even higher latitudes than those presently occupied. In this way, El Niño could exert longer term influences on marine ecosystems in a manner analogous to persistent effects on terrestrial systems (Holmgren et al., 2001). Such a scenario is also consistent with predictions of biome-expansion from the ETP into temperature latitudes in conjunction with global warming (Polovina et al., 2011), which is anticipated to lead to major effects on top pelagic predators (Hazan et al., 2012). D. gigas may already be displaying important changes in distribution and life history that provide a preview of what might be expected for it and ecologically similar, but more slowly responding species, including teleost fishes, in the northeastern Pacific of the future.

Acknowledgements

We thank the many participants who assisted with squid sampling and other activities as well as the captains and crew of research vessels New Horizon (Scripps Institute of Oceanography), BIPXII (CIBNOR, Guaymas) and Pacific Storm (Bruce Mate, Oregon State University Marine Mammal Institute). We also thank the captains and crew of the National Geographic Seabird (Lindblad Expeditions), Don Jose (Baja Expeditions) and Jurel XI and Cesar Salinas for assistance, Xinjun Chen for discussion and sharing data, and Brad Seibel, Chief Scientist for the New Horizon cruises. Bruce Robison is thanked for his support as mentor during HJH’s MBARI postdoctoral fellowship during which this study was undertaken. This work was supported by the National Science Foundation (OCE0851239 to KBB and OCE0526640/0850839 to WFG, California Sea Grant and Ocean Protection Council (ROPFCISH-06), the National Geographic Society Committee of Research and Exploration, the David and Lucile Packard Foundation, the Census of Marine Life’s Tagging of Pacific Pelagics project, the Netherlands Organization for Scientific Research (NWO) and the Schure Beijerinck-Popping Funds (KNAW). We acknowledge support by Stanford University and contributions of the 2010 Holistic Biology class and Jorge Ramos, particularly projects by E. Dannenberg, M. Ream and M. Wachtel and the MS thesis of L. Parassenti.

References


RESPONSE OF JUMBO SQUID TO EL NIÑO 2103


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Effect of the 2009–2010 El Niño on hydrographic properties in the southern Gulf of California.

Figure S2. Quarterly sea-surface temperature (SST) anomalies (°C) during 2009–2011.

Figure S3. Quarterly chlorophyll a (Chl a; mg m−3) anomalies during 2009–2011.

Figure S4. Diet of squid in the Guaymas and Salsipuedes Basins after El Niño.

Figure S5. Potential fecundity of small, mature squid.

Table S1. Sampling details.

Table S2. Sites of CTD casts for water-column profiles.