Characterization of the northernmost spawning habitat of *Dosidicus gigas* with implications for its northwards range extension

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ABSTRACT: The jumbo squid Dosidicus gigas is an ecologically and commercially important species whose northernmost geographic limit is the Gulf of California. However, over the last decades this species has extended its geographic distribution polewards, with associated impacts on the ecosystem. The origin of range-shifting individuals is poorly understood; therefore, we aimed to identify and characterize the northernmost spawning habitat of this species. Implications of the location and oceanographic conditions of the spawning habitats, migration capacity and life history characteristics of *D. gigas* are also discussed to elucidate its migration pattern. The northernmost spawning area was located between the biological activity centres (BACs) around the Gulf of Ulloa at the west coast of southern Baja California Peninsula during winter, summer and autumn 2005. Generalized linear models indicated that the interaction of sea surface salinity and thermocline depth, and the effect of latitude and sea surface temperature explained most of the variability in paralarval presence, whereas chlorophyll a and latitude explained paralarval abundance. Simulations indicated that paralarvae were dispersed towards the southwest or temporarily remained between BACs. The northwards incursion of *D. gigas* may be favoured by BACs and upwelling events along the coast of the northeastern Pacific. In warm years, D. gigas is likely to spawn off the Baja California Peninsula, it may actively migrate as far north as Alaska (USA) tracking BACs and upwelling conditions in search of feeding grounds, and it may return from different areas along the northeastern Pacific to spawn off the Baja California Peninsula.

KEY WORDS: Spawning habitat \cdot Range shift \cdot Biological activity centres \cdot BACs \cdot Jumbo/Humboldt squid \cdot Paralarvae

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INTRODUCTION

The jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) is a commercially and ecologically

important semi-oceanic species that occurs in eutrophic water masses along large-scale oceanic gyres (Aleksandronets et al. 1983 as cited by Nigmatullin et al. 2001). This species occurs over the continental slope and in adjacent oceanic waters of the eastern Pacific Ocean from 25°N to 25°S. The extent of its distribution can reach as far as 3600 nautical miles (n miles) offshore at the equator but is not well understood at polewards latitudes (Nigmatullin et al. 2001). Occasional incursions have occurred off Californian waters since the 1860s (Hatfield & Hochberg 2007). Moreover, arrivals of this species farther north off California (Zeidberg & Robison 2007), Oregon (Litz et al. 2011), Washington (Litz et al. 2011), British Columbia (Cosgrove 2005) and Alaska (Yakutat at ~59°N, Wing 2006) occurred after the El Niño of 1997-1998. The shoaling of the oxygen minimum zone likely represents an expansion of favourable feeding habitat for this species and thus it appears to be associated with the northwards range extension of D. gigas (Bograd et al. 2008, Rosa & Seibel 2010, Stewart et al. 2013a, 2014). In addition, seasonal coastal upwelling (Bograd et al. 2009) may favour the use of the northeastern Pacific as a feeding ground by this species (Ruiz-Cooley et al. 2013).

D. gigas is a short-lived species with a fast growth rate (Mejía-Rebollo et al. 2008), high fecundity (Nigmatullin & Markaida 2009) and extreme plasticity in life-history characteristics (Keyl et al. 2008, 2011, Argüelles & Tafur 2010, Hoving et al. 2013). High horizontal migration capacity (Gilly et al. 2006b, Stewart et al. 2012) and great physiological tolerance (Bazzino et al. 2010, Rosa & Seibel 2010, Gilly et al. 2012, Stewart et al. 2012) allow D. gigas to undergo substantial diel vertical migrations (Gilly et al. 2006b, Rosa & Seibel 2008, Bazzino et al. 2010) to avoid predation and to feed on a wide range of prey from the surface to the oxygen minimum zone (Stewart et al. 2013a). As a consequence, D. gigas may out-compete predators of a similar trophic level or compete with predators of higher trophic levels that are being removed from the range extension zones due to intensive fishing (Caddy & Rodhouse 1998) and environmental variability. The interaction of *D. gigas* with commercial species along the California Current System (CCS) may result in changes in the structure of the ecosystem (Field et al. 2007, 2013, Zeidberg & Robison 2007, Litz et al. 2011). However, the range extension of *D. gigas* may also be an opportunity for commercial and recreational fishers (Field et al. 2007). For instance, approximately 22 000 metric tons of jumbo squid were landed off the west coast of the Baja California Peninsula from 1996 to 2008, an average of 1700 t each year (data provided by SAGARPA-CONAPESCA on request, www.conapesca.sagarpa. gob.mx/wb/cona/cona_anuario_estadistico_de_pesca). Therefore, there is great interest in understanding

the biological and ecological aspects that may facilitate the range extension of *D. gigas* along the CCS and farther north.

An increasing number of studies have aimed to describe the reproductive characteristics (Mejía-Rebollo et al. 2008), migration patterns (Bazzino et al. 2010, Stewart et al. 2012, 2013a,b) and trophic ecology (Field et al. 2007, 2013, Rosas-Luis 2007, Stewart et al. 2013a) of D. gigas along the CCS. Efforts have also been made towards identifying and describing the spawning areas (Camarillo-Coop 2006, Staaf et al. 2013). The main spawning area in the northern hemisphere appears to be the Gulf of California (Gilly et al. 2006a, Staaf et al. 2008, Camarillo-Coop et al. 2011). However, occasional spawning events have also been documented in the Pacific Ocean off the Baja California Peninsula (Camarillo-Coop 2006, Ramos-Castillejos et al. 2010). The first egg mass was found in the wild in the Gulf of California at 16 m depth, and at approximately 26°C, 200 μ mol kg⁻¹ O₂ and 35.5 PSU, with paralarvae hatching at approximately 1 mm of dorsal mantle length (Staaf et al. 2008). Six additional egg masses were found at 9–14 m depth on or near a thermocline in the Gulf of California in May 2015 (Birk et al. 2016). Successful development of artificially fertilized eggs was observed between 15 and 25°C, with the rate of development and the probability of presence of paralarvae increasing at higher temperatures (Staaf et al. 2011, 2013).

Given that temperature may define the limits of the spawning habitat, oceanic warming events are likely to result in northward movements of spawning areas and therefore in the seasonal occurrence of adults farther north of their common distribution. However, to date there is no evidence of *D. gigas* paralarvae farther north of Mexican waters (Staaf et al. 2013). This suggests that reproduction occurs in the Pacific Ocean off Mexico. Planktonic paralarvae and egg masses might then be transported by the currents from spawning areas to enriched feeding areas important for recruitment, e.g. near eddies or upwelling events (Bower et al. 1999, Sakurai et al. 2000), and eventually sub-adult and adult individuals continue the northwards migration if environmental conditions are favourable.

To help understand if *D. gigas* individuals that were spawned in the northeastern Pacific off Mexico are able to undertake polewards incursions as far north as Alaska, we aimed to locate and characterize the spawning areas in the Mexican northeastern Pacific, and to examine the association between the presence and abundance of paralarvae and environmental variables. Based on our findings and building on the literature on the presence, abundance, movement capacity, migratory patterns and life history characteristics of this species along the CCS, we discuss how spawning areas and oceanographic conditions along the CCS may be associated with the northwards range extension of *D. gigas* as far as Alaska.

MATERIALS AND METHODS

Collection of paralarvae

As part of the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) oceanographic campaigns, zooplankton surveys were carried out aboard the RV 'Francisco de Ulloa' at 50 sites in the Pacific Ocean off the Baja California Peninsula each season during 2005 (winter: early February; spring: April-May; summer: July-August; and autumn: October; Fig. 1). IMECOCAL is the Mexican Counterpart of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and has undertaken routine surveys each season since 1997 along the CCS off Mexico (http://imecocal.cicese.mx/). The area of collection was selected based on records of the presence of Dosidicus gigas paralarvae in the Pacific Ocean off Mexico (Camarillo-Coop 2006). A bongo net of 71 cm diameter and 505 µm mesh size



Fig. 1. Area of collection of *Dosidicus gigas* along the Pacific Ocean off Baja California Peninsula during 2005. Sampling sites are indicated with black dots

was used to carry out zooplankton oblique tows to 150 m depth at a constant speed of 2 knots for 10 min, during the day and at night. The volume of water filtered was estimated with a flowmeter located in the centre of the bongo net. Zooplankton samples from IMECOCAL are usually fixed in 4% formalin, except during 2005 when samples were fixed in 99% ethanol and allowed molecular identification of D. gigas paralarvae. Paralarvae of D. gigas are morphologically similar to paralarvae of the purpleback squid Sthenoteuthis oualaniensis, and both species co-exist in Mexican waters; therefore, molecular identification is necessary (Ramos-Castillejos et al. 2010). Mantle length of paralarvae in good morphological condition was measured (n = 77) following Ramos-Castillejos et al. (2010). The abundance of paralarvae was standardized to a volume of 1000 m⁻³ (Smith & Richardson 1979) and abundance intervals were assigned following Smith (1971).

Identification of paralarvae

All paralarvae were identified through genetics; DNA was extracted following the salt-Proteinase K method (Aljanabi & Martinez 1997) from the entire individual or from the mantle only, depending on the size of the paralarvae. A 557 bp fragment of the cytochrome oxidase I (COI) gene was amplified by PCR using buffer solution (22 mM Tris-HCl pH 8.4, 55 mM KCl, 220 µM DNTPs, 3.0 mM MgCl₂), 2.2 U of Tag polymerase (Invitrogen), 0.2 mM of each primer SQ1 (LCO1490) (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and SQ5 (5'-AGG ATG GCA GTA ATA AAG ACA-3'; see Ramos-Castillejos 2007 for further details), 15–25 ng of DNA and ddH_2O to adjust to a final volume of 25 µl. PCR conditions were 94°C for 4 min, followed by 35 cycles of 94°C for 30 s, 46°C for 30 s, 72°C for 60 s and a final step of 72°C for 5 min. The automatic sequencing of a final 369 bp fragment was carried out by SeqXcel Inc. (www. seqxcel.com/).

Oceanographic data

Profiles of temperature (°C), chlorophyll *a* (chl *a*) concentration (mg m⁻³), dissolved oxygen (DO; ml l⁻¹) and salinity (PSU) were recorded aboard the RV 'Francisco de Ulloa' with a CTD SBE-911 plus (Sea-Bird Electronics) at sites where zooplankton tows were carried out. Sea surface temperature (SST) and chl *a* daily data were also obtained from the National

Aeronautics and Space Administration's MODIS Aqua sensor database (https://oceandata.sci.gsfc.nasa. gov/MODIS-Aqua) with a spatial resolution of 4 km. Composite (averaged) images of these data were generated for the survey days where paralarvae were collected.

Association with oceanographic variables

Generalized linear models (GLMs) are useful in modelling associations between cephalopod paralarvae and oceanographic variables (Moreno et al. 2009, Staaf et al. 2013, Otero et al. 2016, Roura et al. 2016). Therefore, GLMs were carried out using the package 'stats' (R Core Team 2014) to explore the associations of presence and abundance of paralarvae, and oceanographic variables and zooplankton tow conditions. Eleven variables were examined: SST, sea surface salinity (SSS), DO, mixed-layer depth (MLD), thermocline temperature (TT), thermocline depth (TD), surface chl a, latitude, longitude, season and natural light conditions at zooplankton tow (light, dark, transition). MLD was defined as the depth at which temperature is 0.5°C less than SST (Monterey & Levitus 1997). TD was defined as the midpoint of the 'maximum slope by difference' in the profile of temperature against depth, and TT was the temperature at TD (Fiedler 2010).

The analyses were performed in a 2-step approach; in the first step, the data were examined as presence and absence of paralarvae (hereafter referred to as paralarval presence) using a binomial distribution with a logit link that included all stations sampled. The most meaningful predictor variables were selected using the 'best', 'forward' and 'backward' automated methods based on the Bayesian information criterion (BIC) with the packages 'leaps' and 'MASS' (Venables & Ripley 2002, Lumley 2009). In the second step, we analysed abundance (hereafter referred to as paralarval abundance) using the Hurdle and the zero-inflated models in the 'pscl' package that account for overdispersion and excess zero counts (Zeileis et al. 2008, Jackman 2015). Hurdle is a 2-component model comprised of a truncated count component (in this case using negative binomial) employed for positive counts, and a hurdle component that models zero vs. larger counts, i.e. positive observations ≥1 (in this case using a binomial distribution). The zero-inflated model is a 2-component mixture model that combines a point mass at zero with a count distribution (in this case using negative binomial). In this model, zeros may come from the

point mass and from the count component (for details see Zeileis et al. 2008). The models were compared using the likelihood ratio test and Akaike's information criterion (AIC), and were selected if they had the greatest log-likelihood and the lowest AIC values. These analyses were carried out in RStudio 0.99.435 (RStudio Team 2015).

Modelling the dispersion of paralarvae

To model the dispersion of particles, i.e. paralarvae, a simple 2D Lagrangian numerical tool (Simple Lagrangian Trajectory Simulator: SimLaTS) was implemented. SimLaTS uses ocean surface velocities derived from a regional numerical model to compute the Lagrangian trajectories of virtually seeded particles (J. A. Kurczyn et al. unpubl. data). The numerical model configuration is similar to that used by Rivas & Samelson (2011) for a domain extending from 20 to 31.75°N and from 120 to 105°W, which includes the Baja California Peninsula and the Gulf of California. The horizontal resolution was 1/12° (~8 km), resulting in a horizontal grid of 158 × 181 points. The vertical resolution consisted of 21 sigma levels with enhanced resolution near the lower and upper boundaries. Monthly data from the Global Ocean Data Assimilation System (GODAS; e.g. Huang et al. 2008, Ravichandran et al. 2013) were used at the open boundaries of the model, i.e. south, north and west. The dailymean wind stress applied to the model's surface was calculated from the 3-hourly wind vector at 10 m height from the North American Regional Reanalysis (NARR; Mesinger et al. 2006) using parameterizations proposed by Smith (1988). The GODAS and the NARR datasets were available on the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory website (ESRL; https://www.esrl.noaa.gov/psd/data). The model simulated 5 yr: the first 4 (2001–2004) were run for spin-up purposes and the final year (2005) was run for the analysis. Surface-velocity outputs were provided every 3 h for the particleadvection method with SimLaTS. These surface velocities include the contributions of several processes like mesoscale quasi-geostrophic dynamics and wind-driven motions.

To model the Lagrangian trajectories, SimLaTS interpolates the model velocity to any prescribed particle's initial position. The particle is then advected using the velocity found for that position and a random contribution related to eddy diffusivity (Smagorinsky 1963, Visser 1997, Saucier et al. 2003, Proehl et al. 2005, Marinone 2006). In general, particle trajectories are governed mainly by the velocity field, but eddy diffusivity also makes a small contribution, where particle positions are computed as:

$$X(t+dt) = X(t) + X_{a}(t) + R_{X}\sqrt{6A_{h}}dt$$
(1)

and

$$Y(t+dt) = Y(t) + Y_{a}(t) + R_{Y}\sqrt{6A_{h}dt}$$
 (2)

where X(t) and Y(t) are the particle positions in the zonal and meridional directions, respectively; $X_a(t)$ and $Y_a(t)$ are the advective displacements obtained by resolving into the velocity field at time t; the velocity is calculated by bilinear interpolation of the instantaneous surface velocity field $\hat{V}(u,v)$ at each particle position; R_x and R_y are uniform random variables with mean = 0 and values that vary between -1 and 1; dt = 3 h is the time lapse (provided by the velocity field), and X(t + dt) and Y(t + dt) are the final positions after summing up all these contributions. Diffusivity coefficients (A_h) are described considering the surface velocity field following Smagorinsky (1963):

$$A_{h} = \gamma \mathrm{d}x^{2} \sqrt{u_{x}^{2} + v_{y}^{2} + \frac{1}{2}(u_{y} + v_{x})^{2}}$$
(3)

where A_h is the diffusivity coefficient (in m² s⁻¹); $\gamma = 0.1$ is the Smagorinsky coefficient; dx is the grid cell size in metres, and u_x , u_y , v_x and v_y are the spatial derivatives of u and v in the x and y direction, respectively.

Fifty particles per location were seeded in the advections, which allowed a more robust analysis of the particles' trajectories because ensembles, instead of individual trajectories, were examined (e.g. Marinone et al. 2004, Jonsson et al. 2009). The implicit chaotic character of the trajectories and small errors that may result from the interpolation are minimized when ensembles are analysed, which reinforces the well-defined patterns observed in the particles' trajectories.

Time and place for the virtually seeded paralarvae in the 30 d Lagrangian simulations correspond to the dates, times and locations of sampling stations where *D. gigas* paralarvae were collected.

Examining the northwards range extension pattern

To describe the northwards range extension pattern of *D. gigas*, an extensive literature review on

ecological and oceanographic aspects of the CCS was carried out. Literature on the life history characteristics of the jumbo squid was reviewed to describe life span, reproductive schedule and size at maturity (Keyl et al. 2008, 2011, Mejía-Rebollo et al. 2008, Argüelles & Tafur 2010, Hoving et al. 2013). Our findings on the spawning habitats and the presence, abundance and dispersion of paralarvae were contrasted with the literature on embryo development, thermal preference and the presence and abundance of *D. gigas* at early stages along the CCS (Yatsu et al. 1999, Camarillo-Coop 2006, Ramos-Castillejos et al. 2010, Staaf et al. 2011, 2013). Likewise, the presence and abundance of sub-adult and adult individuals was reviewed to describe their seasonal occurrence along the CCS (Cosgrove 2005, Wing 2006, Hatfield & Hochberg 2007, Zeidberg & Robison 2007, Litz et al. 2011, among others).

Information on movement capacity was also consulted to describe migratory patterns (Gilly et al. 2006b, Bazzino et al. 2010, Stewart et al. 2012, 2013b, Field et al. 2013). Origins and residency times elucidated by isotopic information (Ruiz-Cooley et al. 2013) and foraging ecology (Field et al. 2007, 2013, Stewart et al. 2013a) were taken into account and contrasted to oceanographic conditions along the coasts of the central and north-eastern Pacific (Lluch-Belda 2000, Bograd et al. 2008, 2009, González-Rodríguez 2008, Kahru & Mitchell 2008).

RESULTS

Distribution and abundance of paralarvae

A total of 234 Dosidicus gigas rhynchoteuthion paralarvae were collected in 34 of 143 zooplankton tows from Punta Eugenia to the Gulf of Ulloa (Table 1). Mantle length ranged from 0.8 to 6 mm, with 40 % of the paralarvae measuring ≤ 2 mm mantle length (Fig. 2). Paralarvae were distributed in the Gulf of Ulloa and near Punta Eugenia and Magdalena Bay during winter, summer and autumn; no paralarvae were found farther north off Punta Eugenia or during spring. The greatest paralarval abundance (58 paralarvae [Pl] 1000 m⁻³) of winter was recorded off the central Gulf of Ulloa within 102 n miles from the coast (Fig. 3A,B). In summer, the greatest paralarval abundance (72 Pl 1000 m⁻³) was recorded off the central and southern Gulf of Ulloa, whereas as few as 4 Pl 1000 m^{-3} were collected at 121 n miles from the coast (Fig. 3C-D). Autumn was characterized by the lowest paralarval abundances, i.e.

Table 1. Summary of the total number of zooplankton oblique tows, number of positive tows where *Dosidicus gigas* paralarvae were present, number of paralarvae and abundance of paralarvae (Pl) per season in the Pacific Ocean off the Baja California Peninsula during 2005

Season	Total tows (n)	Positive tows (n)	Paralarvae (n)	Abundance (Pl 1000 m ⁻³)
Winter	40	11	71	179
Spring	25	0	0	0
Summer	47	15	134	289
Autumn	31	8	29	83



Fig. 2. Mantle length (mm) of *Dosidicus gigas* paralarvae in good morphological condition collected off Baja California Peninsula during 2005 (n = 77 out of 234, see Table 1)

30 and 34 Pl 1000 m⁻³ occurred closer to the coast farther north of the Gulf of Ulloa. However, the lowest record for this season was 2 Pl 1000 m⁻³ at 114 n miles offshore (Fig. 3E–F). According to the scale of abundance of Smith (1971), very low, low and medium paralarval abundances were recorded at every sampling station.

Association with oceanographic variables

Two models were selected to explain the variability in paralarval presence (Table 2). Model 1 included 3 of the 11 variables examined; latitude was the most important variable that explained most of the deviance (13%) and was followed by the interaction between SSS and TD (9%; Table 3). In Model 2, the interaction between SSS and TD was the most important predictor (10% of explained deviance) whereas SST explained 5% of the deviance (Table 3). In both models, the interaction of SSS and TD had a significant influence on paralarval presence, with paralarvae occurring mostly at <80 m TD and between 33 and 34 PSU (Fig. 4A-B). Regarding the variability in paralarval abundance, the zero-inflated model suggested that chl a explained most of the variability in positive counts of paralarvae, whereas latitude, TD and TT explained most of the zero-counts (Tables 4 & 5). In the Hurdle model, latitude explained the positive paralarval counts whilst latitude and TD explained the zero-counts (Tables 4 & 5).

Dispersion of paralarvae

SimLaTS tracks over a period of 30 d for each season exhibited that during winter many particles moved northwards for a short period at the beginning of the simulation. An anticyclone located around 25° N and 114° W also resulted in the transportation of particles towards the northwest at the beginning of the simulation. However, by the end of the 30 d of simulation, most particles mainly moved equatorwards, with particles from sites closer to the coast remaining around the Gulf of Ulloa and Magdalena Bay. In contrast, most particles from offshore sites were dispersed towards the southwest

Table 2. Generalized linear models used to explain the association of the presence of *Dosidicus gigas* paralarvae with oceanographic variables and oblique tow characteristics. Two models were selected: Model 1 = Lat + SSS × TD, and Model 2 = SST + SSS × TD. The models selected had lower values of Akaike's information criterion (AIC). Lat: latitude; SSS: sea surface salinity; TD: thermocline depth; SST: sea surface temperature; df: degrees of freedom associated with each variable; $Pr > |\chi^2|$: p-value of the sequential χ^2 test; Δ AIC: reduction in AIC; AIC (%): percent reduction in AIC from the null model AIC; Δ AIC per df:

Model	Factor	df	$\Pr > \chi^2 $	AIC	ΔΑΙΟ	AIC (%)	ΔAIC per df	Median residual
1	Intercept Lat SSS × TD	142 141 138	1 <0.0001 <0.0001	158.9 141.0 117.4	_ 17.9 23.6	_ 11.3 14.9	_ 0.127 0.171	-0.510 -0.233
2	Intercept SST SSS × TD	142 141 138	1 <0.0001 <0.0001	158.9 153.5 128.8	- 5.4 24.7	_ 3.4 15.5	0.038 0.179	-0.613 -0.355



Fig. 3. Distribution and abundance of *Dosidicus gigas* paralarvae off Baja California Peninsula in relation to chlorophyll *a* (mg m⁻³) and sea surface temperature (SST, °C) during (A–B) winter, (C–D) summer and (E–F) autumn 2005, respectively. Black circles indicate the abundance of paralarvae (Pl) 1000 m⁻³, and arrows indicate the geostrophic currents

(Fig. 5A; see Animation S1 in the Supplement at www.int-res.com/articles/ suppl/m572p179_supp/). Summer simulations showed a dominant southwest trajectory for particles from most locations. Still, some particles were trapped by an anticyclone gyre located around 27° N and 116° W (Fig. 5B; Animation S2). In autumn, the prevailing trajectories also were towards the southwest, although particles from 1 site located at 25.5°N and 115.4°W moved towards the northwest. An anticyclone gyre also was detected around 26°N and 114°W (Fig. 5C; Animation S3).

DISCUSSION

This study identified the Gulf of Ulloa and as far north as Punta Eugenia as the northernmost spawning areas for Dosidicus gigas, with spawning events occurring probably throughout the year. The interaction between SSS and TD appeared to be a good predictor of paralarval presence, but latitude and SST were also of significant importance. In contrast, variability in paralarval abundance was mostly explained by chl a and latitude. Enrichment and seasonal upwelling may benefit the presence of paralarvae between BACs, which seems to favour survival and recruitment (Otero et al. 2008).

The size distribution of paralarvae found in this study suggests that about 40% of the paralarvae were recently hatched; therefore, the southwestern region off the Baja California Peninsula is likely to be a spawning area for D. gigas. In accordance with our findings, Ruiz-Cooley et al. (2013) suggested that one geographic origin of range-shifting individuals likely includes waters of southern Baja California Peninsula. Furthermore, the presence of D. gigas paralarvae around Punta Eugenia were also detected during the El Niño of 1997-1998 (Camarillo-Coop 2006), although it seems plausi-

Table 3. Summary of the selected generalized linear models described in Table 2. Factors are defined in Table 2; deviance (%): % deviance associated with each added variable or interaction; β_i : coefficient estimate; SE: standard error; p: p-value for coefficient estimates

Model	Factor	df	Deviance (%) β _i	SE	р
1	Intercept	142	156.87	365.59251	137.93943	0.008
	Lat	141	12.7	-1.25076	0.31558	< 0.0001
	SSS	140	3.3	-9.86758	4.00559	0.014
	TD	139	6.8	-9.32958	2.97633	0.002
	$SSS \times TD$	138	8.8	0.27607	0.08831	0.002
Tota	al explained (%)	31.6			
2	Intercept	142	156.87	312.7601	125.6876	0.013
	SST	141	4.7	0.3777	0.1484	0.011
	SSS	140	6.4	-9.5184	3.7695	0.012
	TD	139	3.0	-10.1638	2.9331	0.001
	$SSS \times TD$	138	10.2	0.3013	0.0871	0.001
Total explained (%)		24.3				



Fig. 4. Predicted probability of *Dosidicus gigas* paralarval presence as a function of the interaction between sea surface salinity (SSS) and thermocline depth (TD) in the generalized linear models: (A) Presence ~ Lat + SSS × TD and (B) Presence ~ SST + SSS × TD. Lat: latitude; SST: sea surface temperature. The size of the circles represents probabilities between 0.0004 and 1

ble that spawning areas may occur as far north as California during warm conditions (Staaf et al. 2011).

The relaxation of the water flow and deviation towards the Gulf of Ulloa during winter was supported by the dispersion simulation that suggests that paralarvae collected at sites closer to the coast were retained around the Gulf of Ulloa and off Magdalena Bay. However, paralarvae collected at offshore sites were dispersed towards the southwest. Spring is characterized by the southwards flow of the California Current and by strong upwelling that results in surface waters transported offshore. This suggests that paralarvae were transported farther south or west of the sampling stations, which may explain the absence of paralarvae in the area of study and their presence at the entrance of the Gulf of California during this season (Sánchez-Velasco et al. 2016). The presence of gyres during summer suggests the retention of paralarvae off the central-southern Gulf of Ulloa. Accordingly, some paralarvae were dispersed around the Gulf of Ulloa and off Magdalena Bay during the first days of the simulations; however, the main trajectory of dispersion of the paralarvae was towards the southwest. Autumn also was characterized

Table 4. Generalized linear models used to explain the association between abundance of *Dosidicus gigas* paralarvae and oceanographic variables. Factors are defined in Table 2; TT: thermocline temperature; MLD: mixed layer depth; chl *a*: surface chlorophyll *a* concentration; median residual: median residual for the fitted model

Factor	df	Pr>lχ ² l	Log-likelihood	AIC	ΔAIC	AIC (%)	ΔAIC per df	Median residual
Zero-inflated	model							
Intercept	3	1	-205.1	416.2	-	-	_	-
MLD	5	0.150	-203.2	416.4	0.2	480.5	0.04	-0.311
SSS	7	0.0006	-195.9	405.8	10.6	2.5	1.514	-0.251
Latitude	9	0.0002	-187.2	392.5	13.3	3.2	1.477	-0.236
Longitude	11	0.038	-184.0	390.0	2.5	0.6	0.227	-0.220
TD	13	0.024	-180.3	386.5	3.5	0.8	0.269	-0.223
TT	17	0.0006	-172.8	375.6	10.1	2.4	0.594	-0.120
Chl a	15	0.199	-171.2	376.4	8.8	2.1	0.587	-0.155
Hurdle model								
Intercept	3	1	-205.1	416.2	_	_	-	_
TT	5	0.116	-202.9	415.9	0.3	720.8	0.06	-0.304
Latitude	7	< 0.0001	-192.7	399.5	16.4	3.9	2.34	-0.259
TD	9	0.0006	-185.2	388.5	11.0	2.6	1.22	-0.205

Table 5. Summary of the generalized linear models from Table 4. The models selected had greater log-likelihood and relatively lower values of Akaike's information criterion (AIC). Abbreviations as in Tables 2–4

Zero-inflate TD + TT + cl	d model : abundance ~ hl <i>a</i>	MLD + Long	itude + SSS + L	.atitude +
Count mode Factor	l coefficients (negative Coefficient estimate	binomial wit SE	h log link): Z	р
Intercept	40.972	84.729	0.484	0.629
MLD	0.025	0.034	0.726	0.468
SSS	1.403	1.929	0.727	0.467
Latitude	-0.523	0.555	-0.942	0.346
Longitude	0.558	0.374	1.492	0.136
TD	-0.067	0.054	-1.244	0.214
TT	-0.331	0.402	-0.823	0.411
Chl a	-4.479	1.602	-2.796	0.005
Log (theta)	-0.120	0.392	-0.306	0.759
Zero-inflate	d model coefficients (bi	inomial with l	logit link):	
Factor	Coefficient estimate	SE	Z	р
Intercept	81.846	113.516	0.721	0.471
MLD	-0.056	0.040	-1.399	0.162
SSS	-2.942	2.635	-1.117	0.264
Latitude	2.207	0.722	3.056	0.002
Longitude	0.524	0.477	1.099	0.272
TD	0.129	0.056	2.319	0.020
TT	1.015	0.453	2.242	0.025
Chl a	-5.672	3.852	-1.473	0.141
Theta: 0.886	8	AIC: 376.4		
Number of i	terations in BFGS optin	nization: 71		
Log-likeliho	od: –171.2 on 17 df			
Hurdle mod	el: abundance ~ Lat +	TT + TD		
Count mode	l coefficients (truncate	d negative bi	nomial with log	ʃ link):
Factor	Coefficient estimate	SE	Z	р
Intercept	24.617	9.815	2.508	0.012
TT	-0.028	0.246	-0.112	0.911
Latitude	-0.801	0.353	-2.269	0.023
TD	-0.020	0.015	-1.316	0.188
Log (theta)	-0.225	0.386	-0.582	0.560
Zero hurdle	model coefficients (bin	omial with lo	git link):	
Factor	Coefficient estimate	SE	Z	р
Intercept	41.494	10.696	3.879	0.0001
TT	-0.304	0.201	-1.509	0.131
Latitude	-1.355	0.319	-4.245	< 0.0001
TD	-0.044	0.013	-3.372	0.0007
Theta: count	t = 0.7987	AIC: 388.5		
Number of i	terations in BFGS optin	nization: 35		
Log-likeliho	od: –185.2 on 9 df			

by the dispersion of paralarvae towards the southwest. Overall, the dispersion of paralarvae across seasons mainly towards the southwest does not appear to facilitate the northwards range extension of *D. gigas*. Diel vertical migrations may have an effect on the dispersion or retention of paralarvae by using or

avoiding superficial currents as observed in early stages of cephalopods off the Iberian Peninsula (Roura et al. 2016). However, Sánchez-Velasco et al. (2016) detected most D. gigas paralarvae in the upper 20 m of the water column with some paralarvae reaching ~50 m depth, which suggests relatively minor vertical migrations. In addition, the vertical distribution of the paralarvae is within the range of the surface flow of the California Current, which spans from 0 to 200 m depth (Durazo 2015). The Lagrangian model implemented in this study thus appears to be suitable to represent the dispersion of paralarvae of the jumbo squid.

The greater abundance of paralarvae during summer is also supported by upwelling along the Gulf of Ulloa (González-Rodríguez 2008). Cephalopod paralarvae were also associated with eddies and upwelling conditions in the Southern California Bight (Zeidberg & Hamner 2002) and off the Iberian Peninsula (Otero et al. 2016, Roura et al. 2016). Moreover, increasing abundances of ommastrephid paralarvae appear to be associated with upwelling events and eddies in the Gulf of California (Camarillo-Coop et al. 2011, Sánchez-Velasco et al. 2016), in the oriental Pacific (Bower et al. 1999) and in the Mediterranean (Rocha et al. 1999). The classic concept of 'Bakun's Triad' based on enrichment, concentration and retention, provides a framework in which to interpret how changes in geostrophic currents and upwelling intensity can affect the distribution and abundance of D. gigas paralarvae. Upwelling causes enrichment of the waters with food sources that aggregate in sufficient amounts in some areas and that can sustain para-

larvae, sub-adults or adults (Bakun 1996). The reason is that intensified upwelling supports productive conditions that result in increased biomass at all trophic levels (Kang et al. 2002, Otero et al. 2008). Hence, BACs at the Gulf of Ulloa and Punta Eugenia may provide favourable seasonal conditions for spawning thus facilitate the northwards range extension of the population of *D. gigas*. The association between abundance of paralarvae and temperature detected in this study may be a function of the influence that temperature has on

function of the influence that temperature has on embryonic development and spatial-temporal distribution of spawning areas (O'Dor et al. 1982, Boletzky 1987). The embryonic development of ommastrephids often fails below 12.5°C (O'Dor et al. 1982, Yatsu et al. 1999) or stops at early stages of development (Hayashi 1960), extending the period of higher mortality in juveniles and causing poor recruitment (McInnis & Broenkow 1978). The range of SST at which early hatchlings were collected (17.5-23.5°C) is consistent with temperatures where successful embryonic development of D. gigas occurs (15-25°C; Yatsu et al. 1999, Staaf et al. 2011). SST has been suggested as the strongest predictor for presence of ommastrephid paralarvae with zero probability of capturing paralarvae at less than 15°C (Staaf et al. 2013). Furthermore, the presence of paralarvae increases with increasing SST (from 15 to 32°C), even beyond the optimum range of temperature for in vitro embryonic development (Staaf et al. 2011, 2013). The range of SST from 17.5 to 23.5°C may thus delimit the spawning areas of D. gigas, although temperatures as low as 15°C may be tolerated by paralarvae.

early stages. The presence of seasonal upwelling areas along the central and northeastern Pacific may

Molecular identification enabled examining with confidence the association of presence and abundance of *D. gigas* paralarvae only and oceanographic variables within the area of study. However, the presence and abundance of paralarvae may have been underestimated because oblique zooplankton tows appear to collect fewer paralarvae than superficial tows (Staaf et al. 2013). Larger data series are thus desirable and may allow identifying and characterizing broader spawning habitats of *D. gigas*.

Our particle dispersion analysis suggested that *D. gigas* is not dispersed north during the paralarval stage, which is supported by the absence of *D. gigas* paralarvae farther north of Punta Eugenia (Camarillo-Coop 2006, Staaf et al. 2013). Therefore, most of the migration north is likely based on active movement of juveniles and adults. Over a life span of 1.2 yr (Mejía-Rebollo et al. 2008), *D. gigas* may be able to cover approximately 10 000 km mainly because of active migration of adults at average sustained speeds of ~35 km d⁻¹ (Gilly et al. 2006b, Stewart et al. 2012). At 35 km d⁻¹, adult *D. gigas* may be capable of migrating a linear distance of ~4600 km from the

Fig. 5. Simulation of the dispersion of paralarvae of *Dosidicus gigas* for 30 d after their collection during (A) winter, (B) summer and (C) autumn off the Baja California Peninsula during 2005. Stars represent the sampling sites where paralarvae were collected, respective movement trajectories from these sites are shown in different colors

and feeding during normal years. Punta Baja farther north in the Baja California Peninsula may be used occasionally as a spawning and feeding ground during warm years when temperature is suitable for



Gulf of Ulloa, Mexico, to Yakutat, Alaska, in 130 d (Wing 2006, Hatfield & Hochberg 2007, Staaf et al. 2011, Stewart et al. 2012). The size at age for *D. gigas* estimated by Mejía-Rebollo et al. (2008) suggests that individuals are likely to reach waters of Alaska at 300 d of age and ~60 cm mantle length, which corresponds to the size of individuals collected in that area (Hatfield & Hochberg 2007). During the ~120 d remaining of life, *D. gigas* could potentially migrate southwards from Alaska to Mexican waters. However, there is no evidence to support the southwards migration from as far as Alaska. Furthermore, the presence of individuals off Alaska is likely an exceptional migration event due to extreme climatic– oceanographic conditions.

In accordance with the literature, we were able to describe the following size pattern of D. gigas based on the minimum sizes observed at different sites along the CCS and farther north. Recently hatched paralarvae only have been found off the southern Baja California Peninsula (Camarillo-Coop 2006, Ramos-Castillejos et al. 2010), juveniles were recorded off California (Zeidberg & Robison 2007), and larger individuals were collected from the Baja California Peninsula to Alaska (Zeidberg & Robison 2007, Mejía-Rebollo et al. 2008, Litz et al. 2011, Stewart et al. 2012, 2013a,b, Field et al. 2013). This information helped describe the following northwards range extension pattern, more likely to occur during warm events: D. gigas spawns off south-western Baja California Peninsula, or in offshore waters to the west (Ruiz-Cooley et al. 2013). Some hatchlings are likely retained near productive areas, e.g. Magdalena Bay, the Gulf of Ulloa and Punta Eugenia, whereas others are dispersed offshore. Sub-adults may actively migrate northwards at small size (Zeidberg & Robison 2007, Ruiz-Cooley et al. 2013), as well as adults. During the migration north, D. gigas is likely to use BACs and seasonal upwelling as feeding areas along the CCS, e.g. Magdalena Bay, Punta Eugenia, Punta Baja, and off California, Oregon and Washington (Lluch-Belda 2000, Kahru & Mitchell 2008, Bograd et al. 2009, Field et al. 2013, Stewart et al. 2013a). Some individuals may migrate as far north as Alaska during summer and early autumn during extremely warm years. However, most of the population is more likely to stay in regions along the CCS for feeding purposes, as analysis of stable isotopes suggests (Ruiz-Cooley et al. 2013). Finally, large and very likely mature individuals (Field et al. 2013) would return south from along the temperate portions of the CCS during autumn and winter (Stewart et al. 2012, 2013b) to reproduce, whereas some individuals may stay depending on food availability. During warming events such as El Niño, mature individuals may reach and stay around putative spawning areas at 43 or 37° N (Staaf et al. 2011, Onthank & Lee 2013), where the lower temperature limit (15°C) for embryo development may occur during summer and part of autumn (Staaf et al. 2011). Mature squids may migrate to spawning areas off the Baja California Peninsula (Camarillo-Coop 2006, Ramos-Castillejos et al. 2010) (Fig. 6), further sup-



Fig. 6. Hypothetical northward range extension of Dosidicus gigas. In warm years, D. gigas spawns off the Baja California Peninsula throughout the year. Juveniles and adults migrate north, tracking biological activity centres in Mexico (i.e. Magdalena Bay, Punta Eugenia, Punta Baja; Lluch-Belda 2000), and upwelling conditions during spring off California, Oregon and Washington in the USA (Bograd et al. 2009). A portion of the population continues the migration as far north as Alaska during extremely warm conditions, although most individuals are expected to remain off California. Adults and likely mature individuals would return south and remain around the putative spawning areas off California (Staaf et al. 2011, Onthank & Lee 2013), or as far south as off the Baja California Peninsula during autumn and winter in warm years. The migration pattern was reconstructed based on records of D. gigas by Zeidberg & Robison (2007), Litz et al. (2011), Stewart et al. (2012), Field et al. (2013) and Ruiz-Cooley et al. (2013)

ported by increased abundance of paralarvae during summer, autumn and winter off Baja California Sur.

In summary, the life cycle of the northwards rangeextending *D. gigas* could be defined as hatching off the relatively warm Baja California Peninsula, actively migrating north, tracking BACs-upwelling conditions in search of feeding areas mostly off California and Oregon, and returning to waters off the Baja California Peninsula to spawn. The present hypothesis is supported by the seasonal movement pattern proposed by Field et al. (2013).

This study identified and described the oceanographic conditions of what appears to be the northernmost spawning area for *D. gigas* located off the Baja California Peninsula, and contributes to the understanding of the species' northwards extension. Plasticity in life history (Keyl et al. 2008, 2011, Argüelles & Tafur 2010, Hoving et al. 2013) may allow this species to experience rapid adaptation under changing environmental conditions. Therefore, future efforts should focus on determining and comparing the life history characteristics and population dynamics of D. gigas at the historical distribution and current range extension. Further examination of feeding habits of range extending individuals also may help anticipate the potential impacts of the range extension of *D. gigas*.

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