Abstract—Jumbo squid (*Dosidicus gigas*) and purpleback squid (*Sthenoteuthis oualaniensis*) (Teuthida: Ommastrephidae) are thought to spawn in the eastern tropical Pacific. We used 10 years of plankton tow and oceanographic data collected in this region to examine the reproductive habits of these 2 ecologically important squid. Paralarvae of jumbo squid and purpleback squid were found in 781 of 1438 plankton samples from surface and oblique tows conducted by the Southwest Fisheries Science Center (NOAA) in the eastern tropical Pacific over the 8-year period of 1998–2006. Paralarvae were far more abundant in surface tows (maximum: 1588 individuals) than in oblique tows (maximum: 64 individuals). A generalized linear model analysis revealed sea-surface temperature as the strongest environmental predictor of paralarval presence in both surface and oblique tows; the likelihood of paralarval presence increases with increasing temperature. We used molecular techniques to identify paralarvae from 37 oblique tows to species level and found that the purpleback squid was more abundant than the jumbo squid (81 versus 16 individuals).

Distribution of ommastrephid paralarvae in the eastern tropical Pacific

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Adult squid of the oceanic family Ommastrephidae are active generalist predators and key prey for a wide variety of marine fishes, birds, and mammals. They are also the primary targets of the world's larger squid fisheries (Nigmatullin et al., 2001; Markaida et al., 2005; FAO, 2011). Many questions remain unanswered about the reproduction and early life history of these oceanic squid (Young et al., 1985; Boletzky, 2003). Logistical challenges impede direct observation of reproduction and development in the wild, but the collection of paralarvae in net tows often can be used to elucidate ommastrephid spawning grounds and the habitat needs of early life stages (e.g., Okutani and McGowan, 1969; Zeidberg and Hamner, 2002).

Two ommastrephid species that reproduce in the eastern Pacific are *Dosidicus gigas*, the jumbo or Humboldt squid, and *Sthenoteuthis oualaniensis*, the purpleback squid (Vecchione, 1999). The jumbo squid is currently the target of the world's largest squid fishery (628,579 t in 2009 [FAO, 2011]), and commercial interest in purpleback squid is growing (Zuyev et al., 2002; Xinjun et al., 2007). The adult ranges of these 2 species overlap in the eastern tropical and subtropical Pacific (Roper et al., 1984), but the location and extent of spawning grounds of either species over this large region are not well established. Paralarvae of these species cannot be reliably distinguished morphologically; molecular techniques must be used (Gilly et al., 2006; Ramos-Castillejos et al., 2010). When molecular identification is not possible because of formalin preservation or other limitations, paralarvae in this broad geographic region are generally assigned to the "SD complex" (*S. oualaniensis* and *D. gigas* [Vecchione, 1999]).

Ommastrephid paralarvae are relatively rare off California (e.g., Okutani and McGowan, 1969; Watson and Manion, 2011), and none have been attributed to jumbo squid or purpleback squid. Both species, however, have been identified off the Pacific coast of the Baja California Peninsula (Hernández-Rivas et al.[1]; Ramos-Castillejos et al., 2010). With-

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[1] Hernández-Rivas, M. E., R. De Silva-Dávila, S. Camarillo-Coop, J. Granadores-Amores, and R. Durazo. 2007. Ommastrephid paralarvae during 1997–1999 IMECOCAL cruises. Abstract in California Cooperative Oceanic Fisheries Investigations Annual Conference 2007, Program and Abstracts; San Diego, CA, 2–28 November, p. 41. Calif. Coop. Oceanic Fish. Invest., La Jolla, CA.

in the Gulf of California only the jumbo squid has been reported to spawn (Gilly et al., 2006; Staaf et al., 2008; Camarillo-Coop et al., 2011), and, to our knowledge, no other adult ommastrephid has been described from this region, although adults of purpleback squid have been reported from the area near the mouth of this gulf (Olson and Galván-Magaña, 2002). In the southern hemisphere, the Peru Current System has yielded only jumbo squid paralarvae (Sakai et al., 2008). In the large intervening equatorial region, paralarvae of both purpleback squid and jumbo squid are present (Okutani, 1974; Ueynagi and Nonaka, 1993).

The data that form the basis of this knowledge were collected through a variety of methods. Samples from both the Pacific and Gulf coasts of the Baja California Peninsula and from the Peru Current were collected primarily during subsurface oblique tows with bongo nets (Ramos-Castillejos et al., 2010; Camarillo-Coop et al., 2011; Sakai et al., 2008). By contrast, the central region of the eastern tropical Pacific (ETP) has been sampled extensively during surface tows with neuston nets, yielding higher densities of paralarvae (Ueynagi and Nonaka, 1993; Vecchione, 1999). In the ETP, densities can be extremely high, as in the case of more than 10,000 very small paralarvae of the SD complex from a single surface tow conducted during the 1986–87 El Niño (Vecchione, 1999). By contrast, the greatest number of SD-complex paralarvae reported from the Baja California Peninsula is 20, collected with a bongo net (Camarillo-Coop et al., 2011).

Surface tows effectively sample only the top 10–20 cm of the water column, but subsurface oblique tows typically sample from the surface to depths of about 200 m. Because oblique tows sample a broader, deeper range of habitats than surface tows, discrepancies in paralarval abundance and size between the 2 types of tows may reflect different vertical habitat preferences at different stages of development. For example, if recently hatched paralarvae exhibit a preference for surface waters, surface tows would be far more effective at capturing these animals because oblique tows spend very little time at the surface (10–20 cm). And if paralarvae begin to occupy greater depths as they grow, while their numbers decrease because of natural mortality, oblique tows would be likely to capture fewer, larger individuals than would surface tows, as has been seen for the ommastrephid *Todarodes pacificus* (Yamamoto et al., 2002; 2007).

Although high surface abundances can be representatively sampled by surface tows, any narrow subsurface band of high abundance, as might occur at a pycnocline, would be undersampled by oblique tows. However, a strong association of paralarvae with a subsurface feature in preference to the surface could still be detected by a greater likelihood of capture in oblique rather than in surface tows, as has been found for the northern shortfin squid (*Illex illecebrosus*), which shows a relationship with the subsurface interface between slope water and the Gulf Stream in the Atlantic (Vecchione, 1979; Vecchione et al., 2001).

Diel vertical migrations, typical of adult ommastrephids, also could drive different abundances in surface and oblique tows. This result was found in loliginid paralarvae (Zeidberg and Hamner, 2002), but the situation is less clear for ommastrephids (Piatkowski et al., 1993; Young and Hirota, 1990). The few surface tows during which paralarvae of northern shortfin squid were collected in the Middle Atlantic Bight were conducted at night (Vecchione, 1979)— a finding that could indicate a nighttime migration to the surface, but the numbers are too small to strongly support this idea. No significant differences in paralarval abundance of purpleback squid have been found between daytime and nighttime tows in Hawaii (oblique and horizontal tows from the surface to a depth of 200 m; [Harman and Young, 1985]) or Japan (horizontal tows from the surface to a depth of 200 m; [Saito and Kubodera, 1993]).

On cruises conducted by NOAA in the ETP, ecosystem data (including plankton samples) from a large geographic area have been collected regularly and archived for many years. In this study, we present the first analysis of planktonic squid from this data set, focusing on the ommastrephids jumbo squid and purpleback squid. Our aims are 1) to compare surface and oblique tows conducted at the same location and time to determine differences in paralarval distribution and abundance due to sampling method, 2) to address questions of species-specific depth preference and vertical migration, 3) to uncover relationships between paralarval abundance and oceanographic features, and 4) to use molecular techniques on a subset of samples to determine whether the 2 species have distinct spawning areas or habitat preferences within their range overlap. Paralarval distribution is also contrasted with adult distribution data, collected during the 2006 cruise, to confirm that the study region is within the adult range of both species and to enhance our understanding of the ETP as a feeding and spawning area.

Materials and methods

Study area and data collection

The ETP, where the ranges of jumbo squid and purpleback squid overlap, is defined by 3 large surface currents and 2 water masses (Fiedler and Talley, 2006; Fig. 1A). The westward-flowing North and South Equatorial Currents derive from the temperate California and Peru Currents, respectively. The Equatorial Countercurrent flows eastward from the western Pacific to the coast of Central America. These currents define 2 water masses: Tropical Surface Water and Equatorial Surface Water, the latter cooler and fresher than the former. Two smaller-scale oceanographic features are prominent: 1) a distinct thermocline ridge at the interface between the North Equatorial Current and
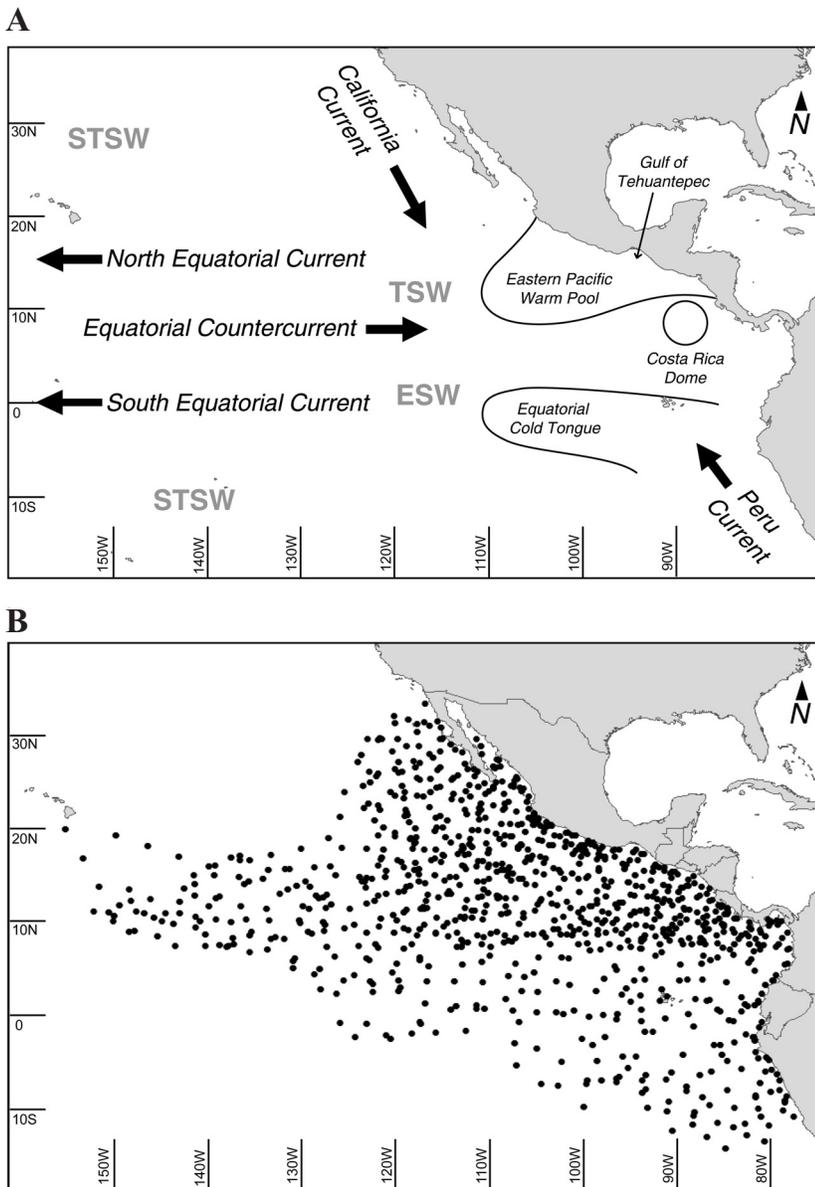
A

B

Figure 1

Map of study area in our examination of the distribution of ommastrephid paralarvae in the eastern tropical Pacific with (**A**) oceanography (after Fiedler and Talley, 2006) and (**B**) sampling stations from cetacean and ecosystem assessment surveys conducted by the Southwest Fisheries Science Center (NOAA) from 1998 to 2006. Two plankton tows, one each with a manta and a bongo net, were conducted each evening approximately 2 h after sunset. STSW=Subtropical Surface Water. TSW=Tropical Surface Water. ESW=Equatorial Surface Water.

the Equatorial Countercurrent, nominally along 10°N latitude (although the exact location varies seasonally) and 2) the Costa Rica Dome, an area of thermocline doming, nominally at 9°N latitude, 90°W longitude, although this feature too varies in location and degree of development through time, seasonally and interannually.

The study area for this research forms a polygon that circumscribes the oceanic waters from the U.S.–Mexico border west to Hawaii, and south to central Peru. Cetacean and ecosystem assessment cruises were conducted in this region by the Southwest Fisheries Science Center (NOAA Fisheries) from late July to early December of 1998, 1999, 2000, 2003, and 2006 (Fig. 1B), with the University-National Oceanographic Laboratory System (UNOLS) research vessel *Endeavor* (1998), and the NOAA Ships *David Starr Jordan* (all years), *McArthur* (1998, 1999, 2000), and *McArthur II* (2003, 2006). Plankton were sampled with 2 types of net tows, conducted ~2 h after sunset each day, for a total of 979 manta (surface) tows and 762 bongo (oblique) tows over the 8-year period. On the *McArthur II* in 2006, during one leg of the cruise, medium-size jigs and rods were used to fish for adult squid from 1 to 2 h after sunset.

Manta nets (Brown and Cheng, 1981) with 0.505-mm mesh were towed for 15 min at a ship speed of 1.0–2.0 kn, with all deck lights off. Bongo nets (McGowan and Brown[2]; Smith and Richardson, 1977), consisting of a pair of circular net frames with 0.505-mm or 0.333-mm mesh, were towed for a 15-min double oblique haul to a depth of ~200 m at a ship speed of 1.5–2.0 kn. The net was lowered continuously at about 35 m/min, held at ~200 m for 30 s, and then was retrieved at about 14 m/min, with the angle of stray always maintained at ~45°.

Volume of water filtered during manta and bongo tows was estimated with a flowmeter suspended across the center of the net. Contents of the codends were preserved in 5% formalin buffered with sodium borate. In 2003 and 2006, the contents of one codend of each bongo tow were frozen in seawater at −20° C, and the contents of the other were preserved in 5% formalin. Also in 2006, the contents of one codend of every fourth bongo tow (38 samples total) were preserved in 70% ethanol instead of formalin.

[2] McGowan, J. A., and D. M. Brown. 1966. A new opening-closed paired zooplankton net. Univ. Calif. Scripps Inst. Oceanogr. Ref. 66-23, 56 p. Scripps. Inst. Oceanogr., Univ. Calif., San Diego, CA.

Water column data were collected with conductivity-temperature-depth (CTD) profilers 1 h before sunrise and 1 h after sunset on each survey day and with expendable bathythermographs (XBTs) during daylight hours at intervals of ~55 km. Samples of surface water were collected in bottles during the CTD casts and in buckets concurrent with XBT casts at depths from 1 to 3 m. Precruise calibration factors (fluorometer calibration factor, F, and acid ratio of pure chlorophyll, τ) were used to calculate chlorophyll-*a* and phaeophytin values from digital fluorometer readings of these surface water samples. Sea-surface temperature (SST) and salinity (SSS) were measured continuously (around the clock) with a thermosalinograph while the ship was underway. Details of the complete data set are available in NOAA data reports (Philbrick et al., 2001, a–c; Ambrose et al., 2002, a and b; Watson et al., 2002; Jackson et al., 2004; 2008).

Sample processing

Cephalopods were removed manually from 654 bongo (1998, 2000, 2003, 2006) and 784 manta (1998, 1999, 2003, 2006) samples. Bongo samples with >25 mL of plankton were fractioned to ~50% of the original sample volume before they were sorted. The absolute count from each tow was divided by the volume of water filtered during that tow, as computed from flowmeter readings, to give paralarvae densities per cubic meter (following techniques described in Kramer et al., 1972).

Adult and paralarval specimens were identified by morphological characteristics (Wormuth et al., 1992). Adults were identified to species by the presence of a fused funnel-locking cartilage in purpleback squid and the absence of the fused structure in jumbo squid. Ommastrephid paralarvae are known as rhynchoteuthions; their distinctive form is recognized easily by the presence of a proboscis. For individuals missing the proboscis or in which the proboscis already had separated into tentacles, identification was based on the characteristic inverted-T funnel-locking cartilage of this family. When proboscis suckers were visible, they were checked to separate individuals of the genera *Hyaloteuthis*, *Eucleoteuthis*, and *Ommastrephes* (enlarged, lateral suckers on proboscis) from individuals of the genera *Dosidicus* and *Sthenoteuthis* (equal-size suckers on proboscis). *Hyaloteuthis*, *Eucleoteuthis* and *Ommastrephes* are relatively rare in the ETP (all the molecularly identified ommastrephids in this study were *Sthenoteuthis* or *Dosidicus*; see also Yatsu[3]), and

only 9 specimens were tentatively identified as *Eucleoteuthis* and 2 specimens were tentatively identified as *Ommastrephes* by proboscis suckers and photophores (6 others were excluded from *Dosidicus* or *Sthenoteuthis* but were too small to be assignable to the other 3 genera). Therefore, any specimens damaged such that the terminal suckers were not preserved were assigned to the SD complex. The presence of paralarvae from other cephalopod families was recorded, but these specimens were not identified to genus or species, or counted.

Morphological techniques for reliable differentiation between paralarvae of jumbo squid and purpleback squid are not available. Wormuth et al. (1992) and Yatsu[3] used proboscis length and photophores as distinguishing characters, but the muscular proboscis can extend and retract (Staaf et al., 2008), and reactions to fixatives have not been quantified. Additionally, there may be variability in ontogenetic timing of photophore formation (Gilly et al., 2006). Ramos-Castillejos et al. (2010) suggested several distinguishing indices that used morphometric ratios; however, samples in this study were prepared in different fixatives (ethanol for jumbo squid and formalin for purpleback squid) that can distort or shrink specimen proportions. The efficacy of indices for diagnoses of individual specimens of unknown species also were not tested. Therefore, we attempted no species-level identification of SD-complex specimens that were preserved in formalin.

Molecular identification of SD-complex ommastrephids from ethanol-preserved samples followed protocols described in Gilly et al. (2006). Two frozen bongo samples were also sent to Hopkins Marine Station for sorting and molecular identification. The frozen samples were selected on the basis of a high abundance of ommastrephid paralarvae in the matching codend, and they were sorted primarily to test whether it is possible to reliably identify paralarvae from a frozen plankton sample.

Mantle lengths (ML) of ommastrephid paralarvae from 1998 manta and bongo tows were measured with an ocular micrometer. For tows with 10 or fewer ommastrephids, all individuals were measured. For tows with more than 10 ommastrephids, 10 individuals were selected for measurement. Selection was arbitrary and aimed to be representative; e.g., the largest (or smallest) specimens were not always included.

Data analysis and modeling

We constructed a data set of ommastrephid paralarval abundance and 5 in situ oceanographic variables: SST, SSS, mixed-layer depth (MLD), temperature at thermocline (TT), and surface concentration of chlorophyll-*a* (CHL). MLD is defined as the depth at which temperature is 0.5°C less than SST (Fiedler, 2010). TT is temperature at the depth of the thermocline as determined by the "maximum slope by difference" method (Fiedler, 2010). MLD, TT, and CHL values were collected from the station nearest the net tow; these data were used

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[3] Yatsu, A. 1999. Morphological and distribution of rhynchoteuthion paralarvae of two ommastrephid squids, *Dosidicus gigas* and *Sthenoteuthis oualaniensis*, collected from eastern tropical Pacific Ocean during 1997–preliminary report. *In* Report of the *Kaiyo Maru* cruise for study on the resources of two ommastrephid squids, *Dosidicus gigas* and *Ommastrephes bartramii*, in the Pacific Ocean, during September 11–December 24, 1997 (A. Yatsu, and C. Yamashiro, eds.), p. 193–206. Fisheries Agency of Japan, Tokyo.

only if the station was located within 18.5 km (10 nautical miles) and was sampled within 12 h of the net tow. SST and SSS were averaged over a 2-h window centered on the time of the net tow. In total, 137 bongo and 164 manta samples were discarded according to these criteria, leaving 517 bongo and 620 manta samples. Many of the discards (56 bongo and 57 manta) were collected aboard the *McArthur* in 2003, when the thermosalinograph malfunctioned. Three outlier points were also removed: an abnormally low value for each of CHL and SST, and an abnormally high value for MLD.

Relationships between ommastrephid abundance and oceanographic variables were explored with generalized linear models in the R statistics package, vers. 2.1.1 (R Development Core Team, 2005). We used generalized linear models because of their utility in modeling relationships between cetaceans and oceanographic habitat (Redfern et al., 2006) and between cephalopod paralarvae and oceanographic habitat off western Iberia (Moreno et al., 2009). Typical of marine survey counts, our paralarval abundance data were overdispersed, with a high proportion of zeros and a few very large samples. Therefore, we followed Aitchison (1955) and Pennington (1983) in performance of a 2-step analysis, in which we separated the data into a binomial presence and absence data set (hereafter referred to as *paralarval presence*) and an abundance data set that included only stations at which paralarvae were present (hereafter referred to as *paralarval abundance*). To analyze paralarval presence, we used a binomial distribution with a logit link; for paralarval abundance we used a lognormal distribution. We used an automated forward/backward stepwise approach based on Akaike's information criterion (AIC) to select the variables for inclusion in the model.

Results

Abundance of paralarvae

Paralarvae of the SD complex were found in 781 of the 1438 formalin-preserved plankton samples. By type of tow, 355 of 656 oblique bongo tows (54.28%) and 426 of 784 surface manta tows (54.34%) contained SD-complex paralarvae. The greatest abundance in a single manta tow was 1588 paralarvae versus 64 paralarvae in a single bongo tow. SD-complex paralarvae taken in bongo tows were distributed over a somewhat broader geographical area than were those paralarvae captured in manta tows (Fig. 2), but density of captured paralarvae was typically at least an order of magnitude greater in manta tows.

Size of paralarvae

Average mantle length in manta tows was 1.94 ±1.29 mm (*n*=779; range 0.7–15 mm ML) versus 1.86 ±1.0 mm (*n*=148; range 0.6–7 mm ML) in bongo tows. No

significant difference was found between these distributions (1-way analysis of variance [ANOVA], *P*= 0.44).

Relationship of presence and abundance of paralarvae to environmental variables and modeling

The stepwise approach for the presence models selected SST, SSS, and TT as predictor variables for manta data, and SST and MLD for bongo data (Table 1). The decrease in the AIC values for these models and the increase in the percentage of explained deviance came primarily from SST for both bongo and manta tows, with minimal contribution from MLD, SSS, and TT. Therefore, SST emerged as the strongest predictor for presence of SD-complex paralarvae, and the probability of capture increased monotonically as SST increased from 15°C to 32°C (Fig. 3).

Analysis of paralarval abundance, rather than presence, revealed no strong predictors (Table 2). For bongo tows, the stepwise approach selected CHL, TT, and SST in the final model (7.5% explained deviance). For manta tows, CHL, SST, MLD, and TT were all selected (12.1% explained deviance). There appears to be little relationship between these variables and nonzero paralarval abundance, which varied over a wide range of each environmental variable for both manta and bongo tows.

Species identification

In total, 97 SD-complex paralarvae were found in 12 of the 38 ethanol-preserved samples. Of these paralarvae, 81 were identified genetically as *Sthenoteuthis oualaniensis* and 16 as *Dosidicus gigas*. Paralarvae of purpleback squid were found over a much greater area than paralarvae of jumbo squid (Fig. 4A). Eight ommastrephid paralarvae were removed from the 2 frozen samples and identified genetically as purpleback squid.

Non-ommastrephid cephalopods were identified in many of the tows, most commonly as taxa in the teuthid families Enoploteuthidae, Onychoteuthidae, Gonatidae, Chtenopterygidae, Cranchiidae, and Brachioteuthidae and in the octopod genera *Argonauta* and *Tremoctopus*; all have previously been reported from the ETP (Ueyanagi and Nonaka, 1993; Vecchione, 1999).

Of the 129 adult squid captured in jigging sessions, 118 were jumbo squid and 11 were purpleback squid. Jumbo squid adults were found primarily in the southernmost sampling sites off Peru, but the few purpleback squid adults were more evenly distributed (Fig. 4B).

Discussion

This study represents the most extensive sampling to date in the ETP of paralarvae of jumbo squid and purpleback squid, covering most of their broad equatorial and subtropical region of range overlap in the Pacific during a period of 8 years.
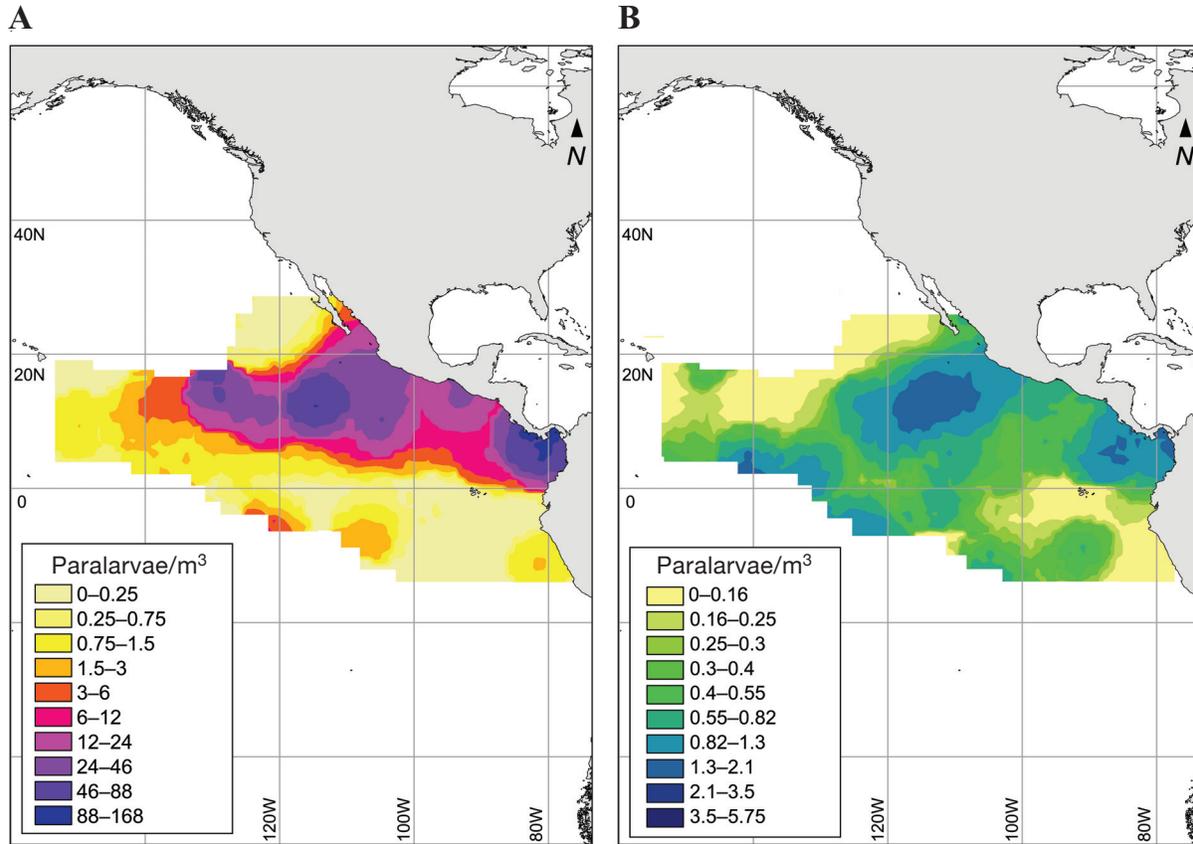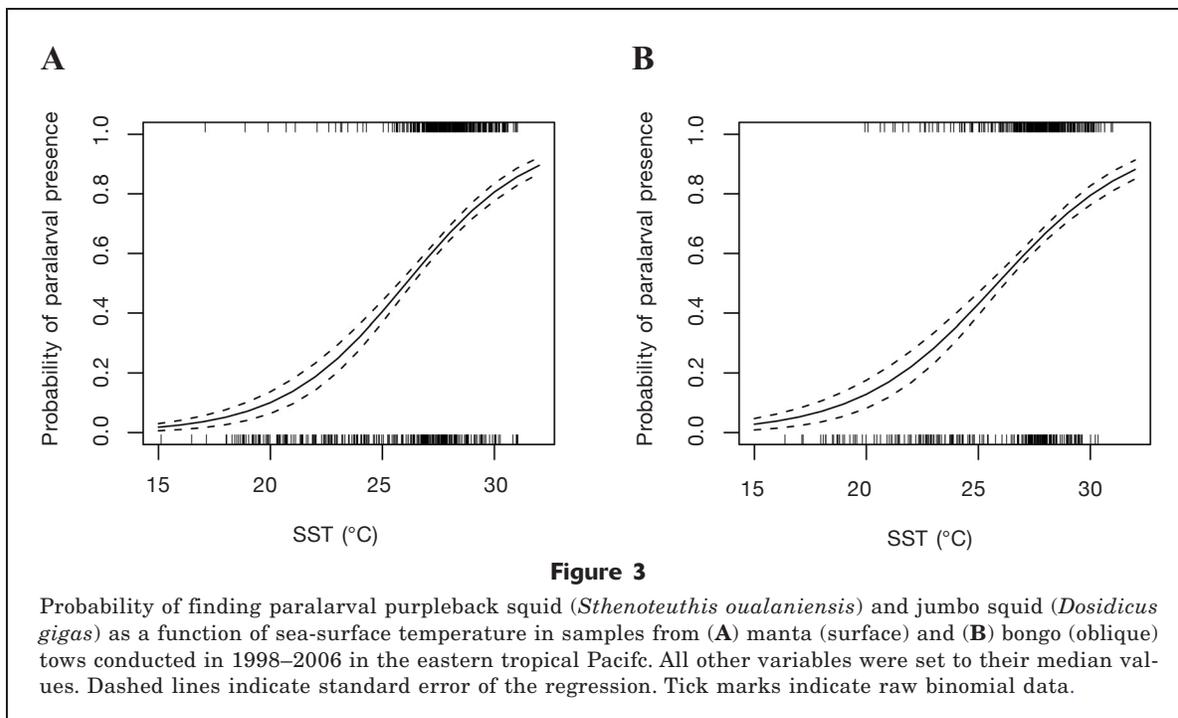
A

Paralarvae/m³
	0–0.25
	0.25–0.75
	0.75–1.5
	1.5–3
	3–6
	6–12
	12–24
	24–46
	46–88
	88–168

B

Paralarvae/m³
	0–0.16
	0.16–0.25
	0.25–0.3
	0.3–0.4
	0.4–0.55
	0.55–0.82
	0.82–1.3
	1.3–2.1
	2.1–3.5
	3.5–5.75

Figure 2

Abundance of paralarval purpleback squid (*Sthenoteuthis oualaniensis*) and jumbo squid (*Dosidicus gigas*) from all study years (1998–2006) for (**A**) manta (surface) and (**B**) bongo (oblique) tows conducted in the eastern tropical Pacific. Paralarval abundance was interpolated by using inverse distance weighting with a cell size of 1° and a fixed search radius of 5°.

Table 1

Generalized linear models used to relate the presence and absence of ommastrephid paralarvae in manta (surface) and bongo (oblique) tows conducted in the eastern tropical Pacific in 1998–2006 to 5 in situ oceanographic variables: sea-surface temperature (SST), sea-surface salinity (SSS), mixed-layer depth (MLD), temperature at thermocline (TT), and surface-concentration of chlorophyll-a (CHL). A stepwise approach selected SST, SSS, and TT for the final manta model; SST and MLD were selected for the final bongo model. Better-fitting models have a higher percentage of explained deviance and a lower Akaike's information criterion (AIC) value.

	Manta				Bongo		
Model	Deviance (%)	AIC		Model	Deviance (%)	AIC
Null		913		Null		710.3
$SST \times SSS \times TT$	18.8	748.1		$SST \times MLD$	12.2	627.7
$SST \times TT$	18.5	748.5		SST	10.6	637.1
$SST \times SSS$	18.4	749.6		MLD	0.2	711.1
$SSS \times TT$	12.7	801.6				
SST	18.1	750.2				
SSS	4.6	873.1				
TT	11	814.9				

Figure 3

Probability of finding paralarval purpleback squid (*Sthenoteuthis oualaniensis*) and jumbo squid (*Dosidicus gigas*) as a function of sea-surface temperature in samples from (**A**) manta (surface) and (**B**) bongo (oblique) tows conducted in 1998–2006 in the eastern tropical Pacifc. All other variables were set to their median values. Dashed lines indicate standard error of the regression. Tick marks indicate raw binomial data.

Vertical distribution of paralarvae

We found no difference in the size of paralarvae between surface (manta) and oblique (bongo) tows, in agreement with Yatsu.[3] These observations are not consistent with an ontogenetic vertical migration to increasing depths within the paralarval stage of development, as proposed for *Todarodes pacificus* (Yamamoto et al., 2002; 2007). This feature, therefore, may not be common to all ommastrephids.

Although *incidence* of capture in surface and oblique tows was nearly identical (54% positive samples in

both), *abundance* of paralarvae was much greater in surface tows. High abundance in surface tows also has been reported for other ommastrephids (Ueynagi and Nonaka, 1993), and extremely high numbers of SD-complex paralarvae have been captured in single surface tows: 819 off Jalisco, Mexico[4] and >10,000 in the

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[4] Palomares-García, R., R. De Silva-Dávila, and R. Avendaño-Ibarra. 2007. Predation of the copepod *Oncaea mediterranea* upon ommastrephid paralarvae in the mouth of the Gulf of California. Abstract i*n* Proceedings of the 1st international CLIOTOP symposium; La Paz, México, 3–7 December.

Table 2

Generalized linear models used to relate nonzero abundance of ommastrephid paralarvae in manta (surface) and bongo (oblique) tows conducted in the eastern tropical Pacific in 1998–2006 to 5 in situ oceanographic variables: sea-surface temperature (SST), sea-surface salinity (SSS), mixed-layer depth (MLD), temperature at thermocline (TT), and surface-concentration of chlorophyll-*a* (CHL). A stepwise approach selected SST, MLD, TT, and CHL for the final manta model and SST, MLD, and CHL for the final bongo model. The resulting percentage of explained deviance and the Akaike's information criteria (AIC) value for these models indicate that none of the oceanographic variables is a strong predictor of nonzero abundance.

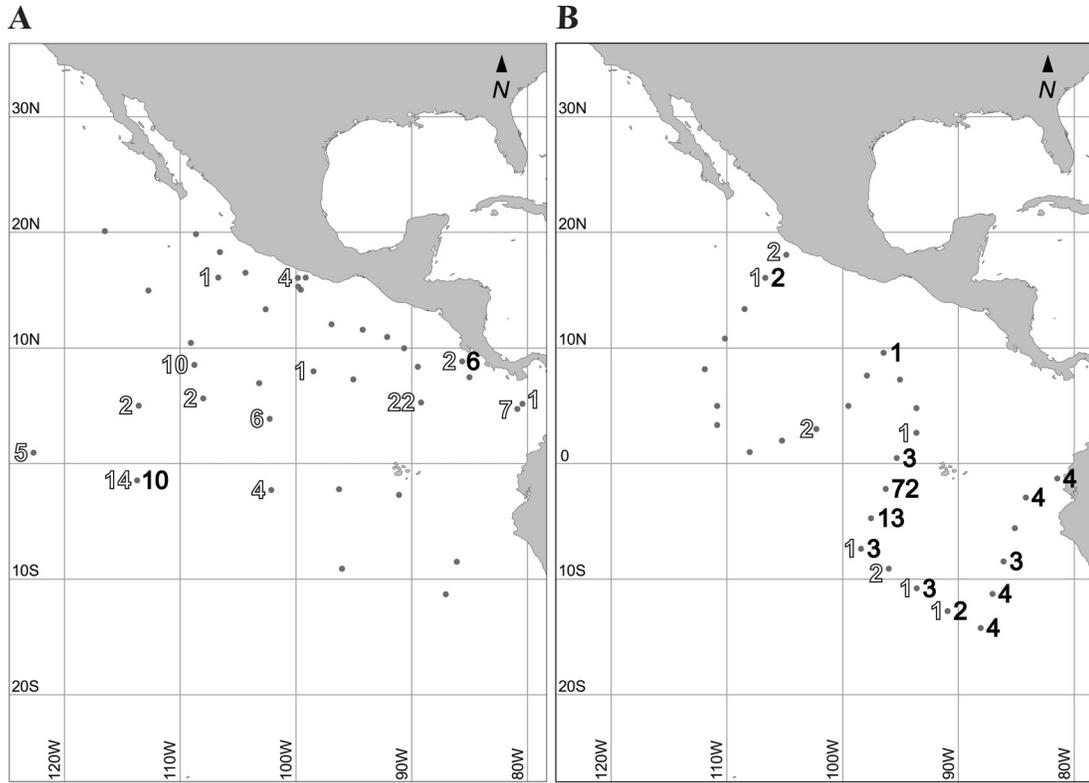| Manta			Bongo		
Model	Deviance (%)	AIC	Model	Deviance (%)	AIC
Null		1341	Null		782
SST × MLD × TT × CHL	12.1	1303.8	*SST × MLD × CHL*	7.5	764.6
MLD × TT × CHL	11.3	1305	*SST × CHL*	6.9	764.8
SST × MLD × TT	11.1	1306	*MLD × CHL*	6.6	765.6
SST × TT × CHL	9.8	1310.9	*SST × MLD*	4.5	772.2
SST × MLD × CHL	9.5	1312.2			

Figure 4

Geographic distribution and abundance of (**A**) genetically identified paralarvae and (**B**) morphologically identified adult ommastrephids caught in the eastern tropical Pacific during surveys conducted in 2006. The numbers at each station (small dot) represent the total number of individuals of purpleback squid (*Sthenoteuthis oualaniensis*) (outlined in black) and jumbo squid (*Dosidicus gigas*) (solid black) captured at that station. At stations where numbers do not appear, no squid were caught.

ETP (Vecchione, 1999). The consistency of this result seems surprising, because ommastrephid egg masses are thought to occur near the pycnocline, typically tens of meters deep, and not at the surface (O'Dor and Balch, 1985). The only reported observation of an in situ egg mass of jumbo squid was in the Gulf of California at a depth of 16 m near the pycnocline (Staaf et al., 2008). Presumably, this characteristic is common to purpleback squid, but we are unaware of descriptions of natural egg masses for this species.

Not only are egg masses of jumbo squid found at depth, but paralarvae are negatively buoyant. Paralarvae in the laboratory can swim to the surface but sink as soon as they stop swimming (Staaf et al., 2008); this negative buoyancy indicates that surface tension is insufficient for passive retention. We can only assume that purpleback squid paralarvae share this trait, and that tissue density of wild paralaravae is similar to laboratory-reared animals.

A preferred surface habitat, in which maintenance of position requires significant energy expenditure, strongly indicates that some benefit is derived from this behavior; the benefit may be access to increased food quantity or to food of higher nutritional value (Yamamoto et al., 2007). Nothing is known of the diet of jumbo squid paralarvae, but amphipods, copepods, and crab zoeae have been found in the digestive tracts of purpleback squid paralarvae (Vecchione, 1991); these and other zooplankton, as well as phytoplankton, also have been found in paralarvae of another ommastrephid, *Illex argentinus* (Vidal and Haimovici, 1998). Furthermore, a case has been made for the use of dissolved and particulate organic material by ommastrephid paralarvae (O'Dor et al., 1985). At certain times and in certain regions, oceanic surface waters may have high concentrations of these foods. The depth of the chlorophyll-*a* maximum in the ETP ranges from 60 to 90 m in open-ocean regions to near the surface in coastal boundary regions (Pennington et al., 2006).

It would be valuable to examine the vertical distribution of paralarvae with systematic oblique or horizontal tows at a series of discrete depths through the upper 100–200 m of the water column at a variety of times in a given area. This approach would give a more accurate picture of habitat use and of any association with the subsurface chlorophyll-*a* maximum or acoustic

scattering layers. To our knowledge, such a dedicated effort to address this problem has not been reported.

Oceanography

The number of both bongo- and manta-net tows that contained paralarvae increased as SST increased from 15°C to 32°C (Table 1, Fig. 3). This increased paralarval occurrence is consistent with the literature. Paralarvae of purpleback squid exhibit a preference for warm temperatures (28–31°C) in waters off Japan (Saito and Kubodera, 1993), and extremely large numbers of SD-complex paralarvae in the ETP were captured in individual tows coincident with the 29°C SST isotherm (Vecchione, 1999). In the Gulf of California, paralarvae of jumbo squid are more abundant during the warm months of June and September (SST of 27.7–29.4°C) than during the cooler season of February and April (SST of 15.3–18.1°C) (Camarillo-Coop et al., 2011). Because our surveys were conducted only between late July and early December, we were unable to assess seasonal variability in paralarval distribution.

We found no evidence for a decrease in paralarval occurrence at the highest SST values, despite the fact that embryonic development in vitro is optimal in the range of 17–25°C and fails to proceed at 30°C (Staaf et al., 2011). The idea that paralarvae may be better able than developing embryos to withstand warmer temperatures would be consistent with a upward vertical migration after hatching. If hatchlings promptly swim from near the pycnocline up to warmer near-surface water, where food may be more readily available, an ontogenetic increase in temperature optima would be advantageous. It also is possible that the upper thermal limit for successful development of wild embryos could be higher than the limit observed in laboratory studies. Embryos studied in the laboratory, particularly those embryos obtained through in vitro fertilization, may perish at high temperatures because of microbial infection, which could be inhibited in the wild by the presence of natural egg jelly (Staaf et al., 2011).

Peak abundances of SD-complex paralarvae observed in our study were an order of magnitude lower than the abundance levels reported during the 1986–87 El Niño (Vecchione, 1999). This discrepancy could be due to chance in sampling or a real difference in abundance. Among our study years, only in 2006 was an El Niño observed, and it was weaker than the one in 1986–87. The other years of our sampling were either in La Niña (1998, 1999, 2000) or neutral (2003) conditions (http://ggweather.com/enso/oni.htm). Year was included in our models as a potential explanatory discrete variable, but it was determined not to be an informative predictor of paralarval abundance or presence, indicating no difference between El Niño, La Niña, and neutral years. However, the strong positive relationship between paralarval occurrence and temperature found in our study is consistent with Vecchione's (1999) hypothesis that the extraordinarily high paralarval

abundances in 1987 were related to the 3.5°C increase in SST during El Niño.

Reduced upwelling during the 1986–87 El Niño led to a 50% decline in chlorophyll-*a* in the region of highest paralarval abundance (Vecchione, 1999). Similarly, in our study, ommastrephid paralarvae were not associated with upwelling zones or their resultant high primary productivity. In general, zooplankton biomass in the ETP tends to be greatest in the 4 major upwelling regions—the Gulf of Tehuantepec, Costa Rica Dome, Equatorial Cold Tongue, and coast of Peru (Fernandez-Alamo and Farber-Lorda, 2006)—but ommastrephid paralarvae were not especially abundant in any of these regions (Fig. 2). Indeed, we found no relationship between SD-complex paralarvae and primary productivity, as measured by CHL or MLD (where the thermocline is shallow, primary productivity tends to be higher [Pennington et al., 2006]).

Species-specific spawning area

Molecularly identified jumbo squid paralarvae have been reported from the Gulf of California (Gilly et al., 2006), off the Baja California Peninsula (Ramos-Castillejos et al., 2010), off Peru (Wakayabashi et al., 2008), and now, in this study, from the ETP. We found that most molecularly identified paralarvae from the ETP were purpleback squid (Fig. 4A), but most adult squid captured by jigging were jumbo squid (Fig. 4B). Although jigging capture rates may have been biased, adult jumbo squid have also been found to outnumber purpleback squid as prey items of the Dolphinfish (*Coryphaena hippurus*) in the ETP (Olson and Galván-Magaña, 2002). Despite this abundance of adult jumbo squid, we found jumbo squid paralarvae in only 2 samples, and these samples also contained paralarval purpleback squid in appreciable numbers (Fig. 4A). Neither the geographic locations nor oceanographic features of these 2 sampling sites were distinct from sites where only purpleback squid was found. Therefore, we can say only that purpleback squid paralarvae appear to be far more abundant than paralarvae of jumbo squid because we have no way of assessing bias in the capture rates of the 2 species during plankton tows.

Species-level molecular identification of paralarvae was possible in this study only with material from oblique tows. If future work on material from surface tows were to find a similar predominance of purpleback squid, it would support the hypothesis that the purpleback squid is the primary ommastrephid that spawns in the ETP. Although jumbo squid can spawn in the ETP or subtropical fringes, its primary spawning grounds may actually lie farther to the north, off the Baja California Peninsula in both the Pacific (Ramos-Catellejos et al., 2010) and Gulf of California (Staaf et al., 2008; Camarillo-Coop et al., 2011), and farther to the south off Peru (Tafur et al., 2001; Sakai et al., 2008; Anderson and Rodhouse, 2001).

This view clearly contrasts with the one originally proposed by Nesis (1983) in which the jumbo squid spawns in the ETP and then migrates to feed at higher latitudes in both hemispheres. Available genetic analysis instead indicates 2 separate breeding populations, 1 in the northern hemisphere and 1 in the southern hemisphere (Staaf et al., 2010). If the preferred spawning habitat of jumbo squid is indeed subtropical to temperate, rather than tropical, it could explain the division into 2 populations, 1 breeding off Mexico and 1 breeding off Peru.

For future collections, we recommend preservation of material from both oblique and surface tows in ethanol. Although we were able to extract and identify paralarvae from frozen plankton samples, the technique has 2 drawbacks: 1) the difficulty of visual identification of individual specimens in the thawed slurry and 2), if the samples are to be sorted in more than one session, the damage done to the entire sample by repeated freeze-thaw cycles.

Conclusions

We found paralarvae in surface and oblique tows to be of equal size, indicating that paralarvae of the 2 ommastrephid species jumbo squid and purpleback squid do not engage in ontogenetic vertical migration at the paralarval stage. Ommastrephid paralarvae were much more abundant in surface tows than in oblique tows; this finding may indicate an ecological advantage of surface waters—perhaps, related to feeding. Models selected SST as the strongest predictor of paralarval presence in both surface and oblique tows; presence was more likely at higher temperatures. Therefore, warm surface waters appear to be the preferred habitat of ommastrephid paralarvae in the ETP. Molecular identification of specimens from a small subset of oblique tows showed that paralarvae of purpleback squid far outnumbered those of jumbo squid in this region. Adults of purpleback squid are broadly distributed in the tropics, whereas adult jumbo squid are abundant in tropical, subtropical, and temperate waters and occasionally present in boreal waters. Results from this study are consistent with the possibility that the purpleback squid spawns primarily in the tropics, and the jumbo squid spawns preferentially in subtropical or, perhaps, even temperate regions.

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