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Essential market squid (Doryteuthis opalescens) embryo habitat: A baseline for anticipated ocean climate change

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ESSENTIAL MARKET SQUID (*DORYTEUTHIS OPALESCENS*) EMBRYO HABITAT: A BASELINE FOR ANTICIPATED OCEAN CLIMATE CHANGE

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ABSTRACT The market squid *Doryteuthis opalescens* deposits embryo capsules onto the continental shelf from Baja California to southern Alaska, yet little is known about the environment of embryo habitat. This study provides a baseline of environmental data and insights on factors underlying site selection for embryo deposition off southern California, and defines current essential embryo habitat using (1) remotely operated vehicle–supported surveys of benthos and environmental variables, (2) SCUBA surveys, and (3) bottom measurements of T, S, pH, and O_2. Here, embryo habitat is defined using embryo capsule density, capsule bed area, consistent bed footprint, and association with $[O_2]$ and pH (pCO_2) on the shelf. Spatial variation in embryo capsule density and location appears dependent on environmental conditions, whereas the temporal pattern of year-round spawning is not. Embryos require $[O_2]$ greater than 160 μmol and pH_T greater than 7.8. Temperature does not appear to be limiting (range: 9.9°C–15.5°C). Dense embryo beds were observed infrequently, whereas low-density cryptic aggregations were common. Observations of dense embryo aggregation in response to shoaling of low $[O_2]$ and pH indicate habitat compression. Essential embryo habitat likely expands and contracts in space and time directly with regional occurrence of appropriate O_2 and pH exposure. Embryo habitat will likely be at future risk of compression given secular trends of deoxygenation and acidification within the Southern California Bight. Increasingly localized and dense spawning may become more common, resulting in potentially important changes in market squid ecology and management.

KEY WORDS: squid, essential fish habitat, oxygen, embryo exposure, Loliginidae, *Doryteuthis opalescens*, climate change, ENSO

INTRODUCTION

Market squid *Doryteuthis opalescens* range in the North East Pacific from Baja California Sur, Mexico, to Southeast Alaska, United States (Okutani & McGowan 1969, Wing & Mercer 1990). Essential habitat is defined within the Magnuson–Stevens Act (United States) as ''waters and substrate necessary to fish (including invertebrates) for spawning, breeding, feeding, or growth to maturity.'' Market squid deposit their embryo capsules predominantly onto sandy seafloor habitats on the continental shelf (<100 m depth; Bernard 1980, Street 1983, Zeidberg et al. 2011), which presently represents a coarse definition of essential habitat for this species. Utilization of soft bottom habitats may be partly due to the availability of extensive sandy plains on the shelf (Revelle & Sheppard 1939) and that adult squid may have no strong affinity toward a particular sandy habitat (Young et al. 2011).

Market squid are a forage species (Morejohn et al. 1978) within the California and Alaska current systems. This species currently supports an important commercial fishery in California (Porzio 2013) and was proposed as the target of a new commercial fishery in Southeast Alaska in 2018. Economic exploitation of market squid began in Monterey in the 1850s by Chinese immigrants, later expanding to include Italian immigrants, and developed into a major fishery in the 1970s (Vojkovich 1998, Brady 2008). Since the 1990s, the commercial fishery has thrived in the Southern California Bight (SCB) (Vojkovich 1998, Brady 2008, Porzio 2015). Market squid have been commercially harvested at or close to the present annual quota of 107,048 m tons from the 2010 to 2011 through the 2014 to 2015 seasons (Porzio 2015) and, in 2014, constituted ~64% of the entire biomass of all the marine species captured and 30% of the ex-vessel value for all landings off California (Porzio 2015). The relative importance of catch among California fisheries switched from fish to invertebrates in the 1990s, and the importance of invertebrate fisheries has steadily increased (Rogers-Bennett & Juhasz 2014). Therefore, fishery trends in California reflect global patterns of fishing down food webs (Pauly et al. 1998, Pauly & Palomares 2005). Overfishing has decreased vertebrate predators of squid, thus, releasing controls on nearshore squid populations (Caddy 1983). This has resulted in the expansion of squid fishing especially in response to shortages of finfish (Arkhipkin et al. 2015).

The greatest abundances of embryo capsules in the SCB have been reported at temperatures between 10°C and 14.4°C (Zeidberg et al. 2011). The majority of commercial fishing for market squid off California occurs in the SCB (Porzio 2015) where pH and $[O_2]$ decrease nonlinearly with depth and are predicted to decline with a changing climate (Gruber et al. 2012, Takeshita et al. 2015) in addition to periodic stress associated with El Niño Southern Oscillation (ENSO) (Turi et al. 2018). The compression of rockfish habitat has already been attributed to decreased $[O_2]$ and pH (McClatchie et al. 2010). These declines have also been shown to slow the development of mussel larvae (Frieder et al. 2014) and squid embryos (Navarro et al. 2014, 2016, Pierce 2017).

Fishery-independent surveys of market squid embryo capsules in the SCB were last conducted in the 1950s (McGowan 1954, Okutani & McGowan 1969). Recent surveys of commercially fished areas suggest that areas used by squid embryos (Zeidberg et al. 2011) and paralarvae (Koslow & Allen 2011, Van Noord & Dorval 2017) are exposed to waters containing low $[O_2]$ and pH. If so, impacts on squid populations would

likely also affect other species. As a forage species, market squid are an energetically integral part of the ecosystem both as predator and prey. Market squid predators include finfish, seabirds, and marine mammals (Morejohn et al. 1978). Thus, the characterization of [O$_2$], pH, and temperature conditions preferred by squid for capsule deposition is necessary for defining essential habitat.

Market squid have high growth rates and a short generation time (usually 6–8 mo; Yang et al. 1986, Jackson & Domeier 2003). Spawning ages of squid are highly dependent on oceanographic conditions (e.g., ENSO), ranging from ~4.5 mo (129–137 days) to ~8 mo (225–257 days; Jackson & Domeier 2003). Market squid are semelparous (Fields 1965), death occurs within a week of spawning, and most viable embryos are deposited on the first day of spawning (Perretti et al. 2015). Fast growth rates and a short generation time likely enable market squid populations to respond rapidly to changes in oceanographic conditions (Jackson & Domeier 2003, Zeidberg et al. 2004, Pecl & Jackson 2008, Koslow & Allen 2011).

Observations of market squid spawning occur primarily from October to May in the SCB (Henry et al. 2005), and occur within the same areas and habitats each spawning season (Fields 1965, Vojkovich 1998, Zeidberg & Hamner 2002). Fields (1965) found that market squid consistently deposit embryo capsules at or immediately next to aerated seawater inflow in the laboratory, suggesting water motion and elevated levels of [O$_2$] and pH (low pCO$_2$) are important cues for site selection.

Over large scales, embryo habitat for market squid are estimated to likely encompass much of the continental shelf off California (Zeidberg et al. 2011), the central coast of Canada (Bernard 1980), and Southeast Alaska (Street 1983). In the SCB, which may regularly comprise the largest portion of the commercial fishery biomass for market squid (Dorval et al. 2013), environmental conditions vary among years, seasons (Hickey 1979, Checkley & Barth 2009, Send & Nam 2012), and days (Frieder et al. 2012) and can be strongly event-based (Nam et al. 2011). *In situ* physicochemical conditions that embryos are exposed to during their development are presently not known, including how squid embryo habitat is influenced by seasonal, event, and daily variation.

OBJECTIVE

The overall objective of this study was to develop methods to evaluate the essential embryo habitat of market squid *Doryteuthis opalescens*, with particular attention to physicochemical characteristics. This study defines essential embryo habitat using two main characteristics: (1) sites frequently selected by spawning squid for egg deposition and (2) the physicochemical climate of such realized embryo habitat. Site selection is a key determinant, as spawning squid presumably deposit embryos in areas that optimize the development of their progeny, and hence, provide a means to understand which habitats squid use. Thus, this study defines the realized squid embryo habitat on biotic and chemical environmental attributes in time and space, and characterizes benthic capsule environmental exposures in these locations.

MATERIALS AND METHODS

Spawning Site

Market squid regularly use the same areas for spawning throughout their range (Shimek et al. 1984, Jefferts et al. 1987,

Young et al. 2011). This study was conducted in northern La Jolla, San Diego, CA (hereafter referred to as NLJ; 32.86° N, 117.28° W), where squid embryos have been consistently observed, and spawning aggregations have been known to commercial squid fishers since the early 1900s. This site also has the longest history of *in situ* scientific observation of market squid embryos throughout their range (McGowan 1954, Okutani & McGowan 1969).

Temperature and salinity have been recorded at the nearby (~1 km) Scripps Institution of Oceanography pier since 1916 (McGowan et al. 2010). Environmental measurements, including pH, [O$_2$], salinity, temperature, and density from the surface to the lower continental shelf have also been monitored nearby (within ~6 km) since 2005 (Del Mar mooring, NNW, 32.93° N, 117.31° W; Nam et al. 2011, Send & Nam 2012). The carbonate chemistry of seawater near the seafloor has been characterized and the rates of ocean acidification have been predicted up to the year 2100 for the area (Takeshita et al. 2015). Geologically, the seafloor in La Jolla has been described (Le Dantec et al. 2010, Switzer et al. 2016) with particular consideration for the La Jolla submarine canyon complex (Paull et al. 2013). Many known squid spawning habitats are found next to submarine canyons. Northern La Jolla is regularly used by squid for spawning, and NLJ is where the biological study of market squid embryo beds first began (McGowan 1954, Okutani & McGowan 1969). The largest squid embryo bed reported (1.76 × 10^{12} embryos) was observed at this site, estimated to have covered an area spanning 1.6 × 10^7 m^2 (Okutani & McGowan 1969). Importantly, these records were completed before squid were targeted in the SCB by the commercial fishery (Vojkovich 1998).

Environmental Data Acquisition within Embryo Habitat

Comprehensive environmental data from within the squid embryo bed were documented from August 30, 2012 to October 21, 2013 at the NLJ site. A SeapHOx instrument (Martz et al. 2010, Bresnahan et al. 2014) was stationed 0.5 m above the seafloor to measure seafloor water characteristics (see Fig. 1 for instrument location). The SeapHOx recorded T, S, pressure, O$_2$, and pH$_T$ every 15 min between June 23, 2012 and July 4, 2013, spanning four deployments. A SeaBird MicroCAT CTD (SBE 37SMP-IDO) mounted on the remotely operated vehicle (ROV) used for surveying the benthos recorded T, S, P, and O$_2$ at 1-min intervals (Figs. 1 and 2). Temperature and [O$_2$] were used to estimate pH$_T$ based on Alin et al. (2012).

Biological Data Acquisition

Biological data were acquired on the inner shelf (10–100 m depth, Fig. 1) using a Seabotix LBV150 ROV equipped with two external light-emitting diode lights (1,080 lumen, 140 deg beam angle) and red scaling lasers separated by 5 cm (Switzer et al. 2016). Squid embryo capsules were collected using SCUBA on 19 days distributed throughout the study period (May 2012 to January 2014; Navarro 2014). Taxon-specific depth and spatial data were developed from ROV video surveys of seafloor megafauna. Surveys were temporally stratified to include upwelling
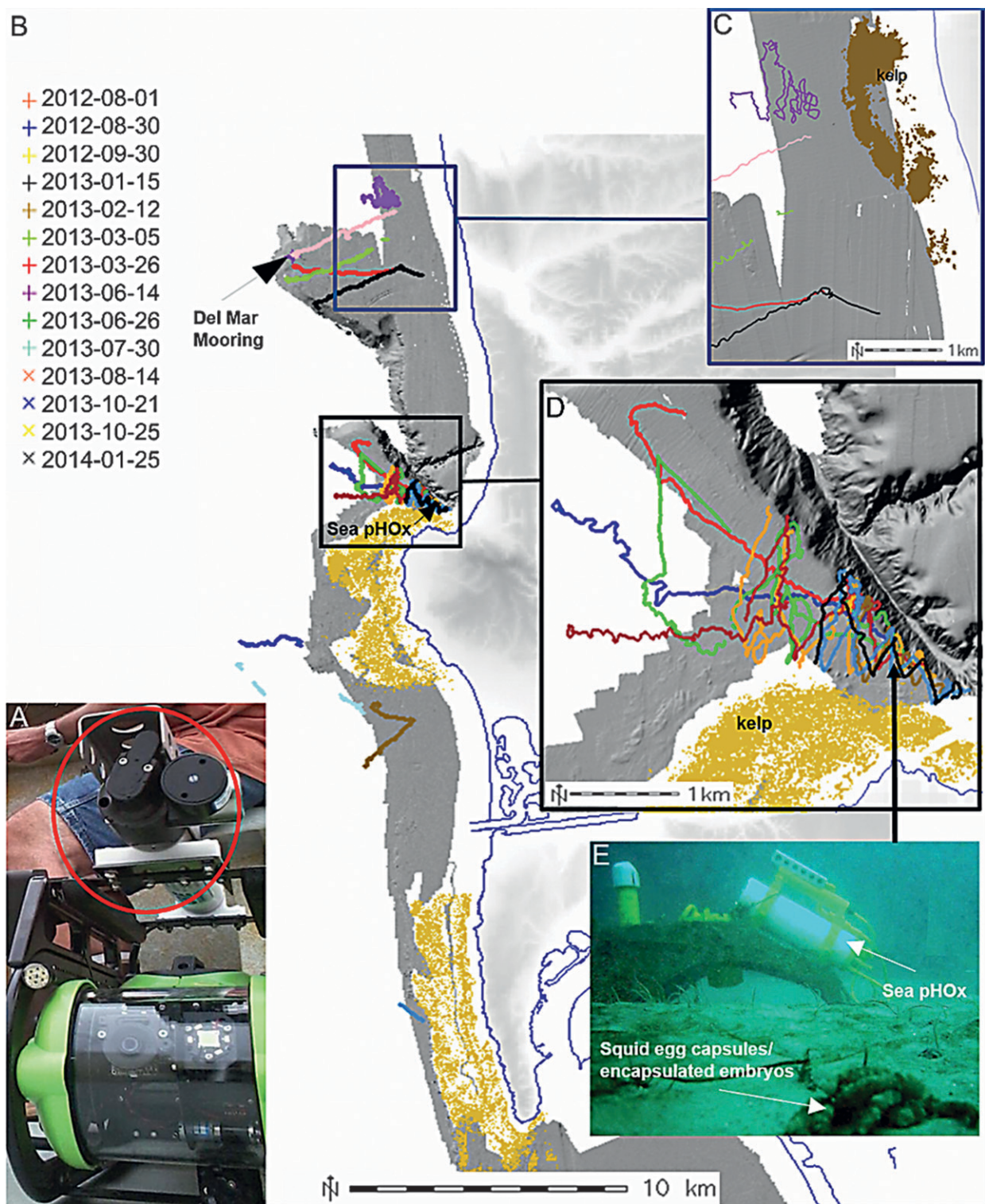
Figure 1. Map showing study locations offshore of San Diego County, United States. The ROV, Seabotix 150, with an attached SeaBird CTD and O_2 sensor circled in red (A). Remotely operated vehicle survey tracks are color coded to indicate survey date (B). Magnified view of survey tracks offshore of Solana Beach with kelp forest shown in brown (C). Magnified view of survey track offshore of Point La Jolla with kelp forest indicated in gold (D). Picture of the SeapHOx instrument at 30 m depth within squid embryo habitat (E).

(spring and summer) and non-upwelling (fall and winter) seasons. Areas of embryo beds were extrapolated from ROV tracks, and densities were estimated from counts of mops (capsule aggregations) and isolated embryo capsules at 5 sec intervals. Mop sizes were categorized by the number of capsules using a $\log_4$ classification ("small" ≤ 4, 5 ≤ "medium" < 24, and 25 ≤ "large" < 125 capsules). Density was averaged for each survey ($n = 18$) and multiplied by
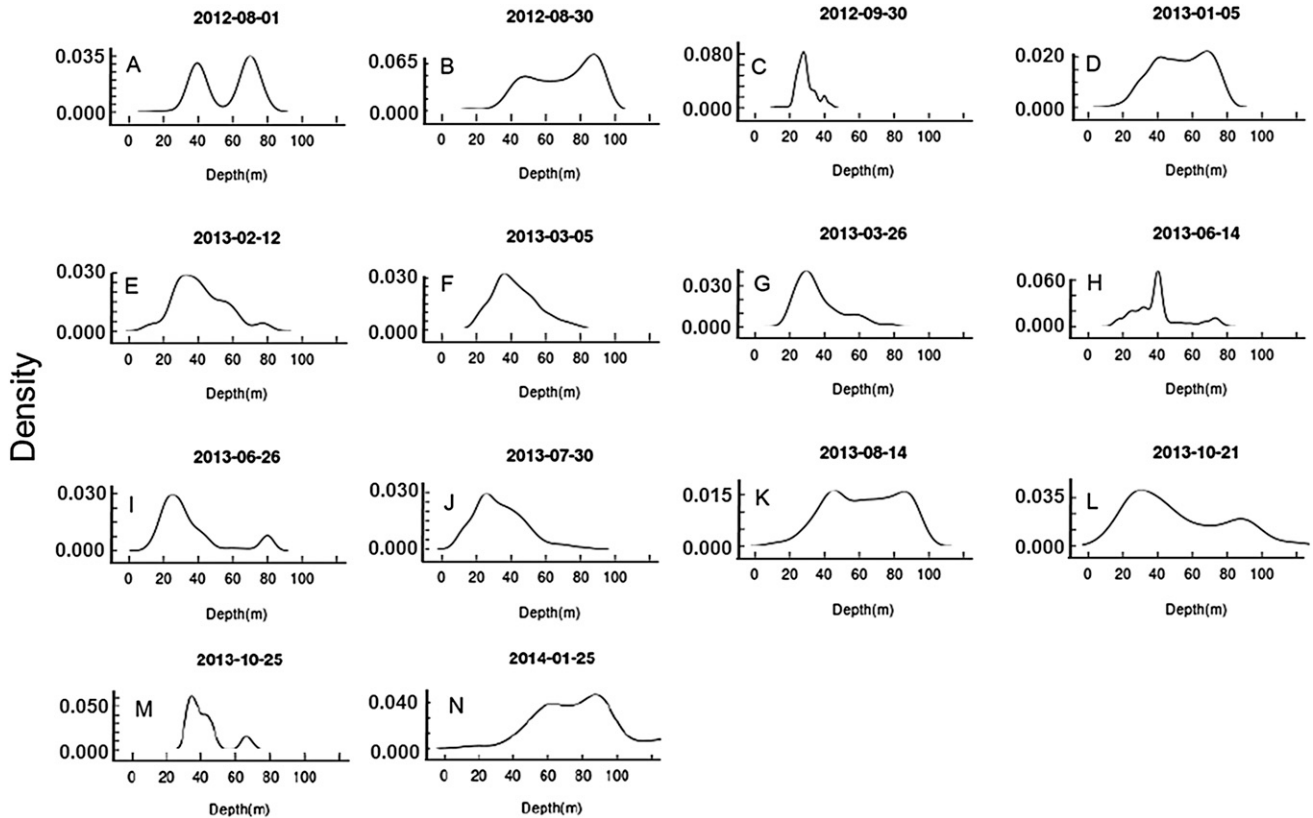
Figure 2. Probability density distributions of surveyed depth (m) per ROV survey date. (A). August 1, 2012. (B). August 30, 2012. (C). September 30, 2012. (D). January 5, 2013. (E). February 12, 2012. (F). March 5, 2013. (G). March 26, 2013. (H). June 14, 2013. (I). June 26, 2013. (J). July 30, 2013. (K). August 14, 2013. (L). October 21, 2013. (M). October 25, 2013. (N). January 25, 2014.

track survey area to estimate capsule totals. A regression model was used to estimate seasonal squid embryo counts from embryo collections (Navarro 2014) because the number of embryos per capsule has been shown to vary (McGowan 1954, Fields 1965, Zeidberg et al. 2011). Embryo abundance was calculated as the product of total capsule count and the number of embryos per capsule.

RESULTS

Essential Squid Embryo Habitat

Oxygen, pH, and S were continuously measured within embryo habitat for the first time, and temperature was measured *in situ* throughout embryogenesis across multiple cohorts. Previously, studies of embryo capsule habitat at any given site were limited to hours or days. This study mean observed values of oxygen, pH_T, S, and T were 187 µM ($\pm$52 µM), 7.88 ($\pm$0.12), 33.5 ($\pm$0.1), and 12.5°C ($\pm$1.7°C), respectively ($\pm$1 SE), when squid were present ($n = 713$; Table 1). Depth distributions of oxygen varied considerably among days that ROV surveys were conducted (Figs. 3 and 4).

Squid embryo habitat was concentrated in the shallow margins of the shelf (<35 m), usually next to, but not within kelp forests [see Fig. 5 for ROV survey tracks, hill-shaded topography, and kelp forest distributions from Parnell (2015)]. The distribution of embryos observed during ROV surveys is shown in Figure 6. Embryo depths were highly variable and ranged

from 10 to 92 m (Fig. 7, Tables 2 and 3). Essentially, embryo habitat was limited to zones of high O_2 and pH ($[O_2]$ > 160 µmol kg^{-1}, pH_T > 7.8). Temperature, O_2, and pH were always the highest and salinity was the lowest at shallow depths (<35 m). The deepest limit of embryo distribution was dynamic, once extending to greater than 90 m. This extension co-occurred with the depth expansion of elevated O_2 and pH. Embryo beds were observed during most surveys at NLJ (eight of nine surveys) at depths less than 50 m, whereas the embryo beds were observed on only five of nine surveys at depths greater than or equal to 50 m (Tables 2 and 3). The deeper limit of squid embryo habitat ranged from 33 to 91 m and the shallow boundary ranged from 10 to 33 m. Embryo habitat was highly structured and easily observed in the shallows when T, O_2, and pH at depth were at annual lows. By contrast, embryos were more difficult to observe (i.e., pseudo-cryptic) and found at all depths of the shelf when T, O_2, and pH were at annual highs. Environmental conditions within and outside of embryo beds were significantly different ($P < 0.0001$ for depth, temperature, salinity, oxygen, Wilcoxon test; Table 1).

Adequate densities of spawning aggregations are vital for marine predators and fishers to detect the spawning occurrence of squid. In this study, embryo habitat was dense ($\geq$2 embryo capsules/m^2; Fig. 8, Table 3), primarily, when the shelf had relatively low $[O_2]$ (<135 µM; Fig. 6) and pH. During these periods, squid aggregated to those areas with the highest available $[O_2]$ and pH, and contracted to depths of less than or equal to 40 m. Embryo capsules were much less dense

TABLE 1.

Environmental factors in and out of *Dorteuthis opalescens* embryo beds from ROV surveys (August 1, 2012 to July 30, 2013; depth range = 11.2–94.5 m).

Stat.	T (°C)	T (°C)	[O_2] (µM)	[O_2] (µM)	pH_{est}	pH_{est}	D (m)	D (m)	S	S
AVG	11.63	*12.49*	161.6	*186.7*	7.818	*7.876*	45.5	*35.6*	33.57	*33.51*
SD	1.45	*1.71*	47.1	*52.2*	0.103	*0.116*	19.7	*13.1*	0.12	*0.12*
MAX	16.45	*15.46*	276.9	*266.3*	8.110	*8.060*	94.4	*91.5*	33.93	*33.90*
MIN	9.59	*9.87*	84.4	*88.2*	7.660	*7.670*	11.2	*11.3*	33.35	*33.31*
N	1,101	*713*	1,101	*713*	1,101	*713*	1,101	*713*	1,101	*713*
χ^2		118.6		93.4		104.4		120.2		114.2
P		***<0.0001***		***<0.0001***		***<0.0001***		***<0.0001***		***<0.0001***

pH was estimated using temperature and oxygen data (Alin et al. 2012). Underlined = data acquired when *D. opalescens* embryo capsules were absent; Italicized = data acquired when *D. opalescens* embryo capsules were present. Bold and italicized = significant. AVG = average, MAX = maximum, MIN = minimum, *N* = number of samples.

(<2 embryo capsules/m^2) when O_2 and pH_T were the greatest ([O_2]: 160.2–276.9 µM, pH_T: 7.81–8.11; Table 3). Capsules were observed broadly across the shelf at depths below 40 m during these conditions.

Continuous measurements of pH_T, T, S, and [O_2] within squid embryo habitat were highly variable both years (Fig. 9). This variability occurred primarily at semidiurnal (M2) and diurnal (K1) periods (Fig. 10). Power spectra of SeaHOx T, O_2, and pH were consistent with M2 and K1 internal wave propagation on the shelf.

Substrate Selection

Adults attached their embryos to various soft and hard substrates during the study. Most observations of embryos occurred over unconsolidated substrata, with most of these observations occurring on sand (~2 ≤ φ ≤ 3) as opposed to silts and muds (φ > 5). Embryo capsules were observed across sandy bedforms including flats, ripples, and waves. Although surveys over submarine canyon walls were only conducted when embryos were observed as deep as the canyon rim, observations indicate that squid embryo capsules were often present and only
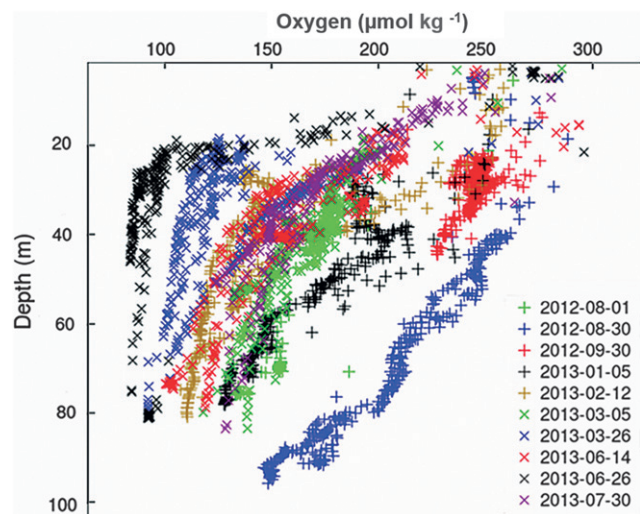

Figure 3. Dissolved oxygen concentrations as a function of depth observed during ROV surveys of the continental shelf. Data points are coded to distinguish the date of the survey by a combination of symbols and color.

at slightly lower densities than on the shelf above the canyon (average density = 4.23 capsules/m^2). Submarine canyon walls were the most used hard substrate for embryo deposition (five of five ROV surveys). On the submarine canyon walls, market squid attached capsules onto horizontal and vertical surfaces of rocks and within rock crevices. Market squid were observed attaching their capsules to lone kelp stipes outside of the kelp forest and to artificial substrates, including scientific instruments in the study area.

Biotic Associations

Biotic interactions between squid embryos and other benthic species were commonly observed. Embryo capsules were frequently observed with other shelf biota including *Diopatra* spp. (polychaete: 2.3% of observations), *Astropecten* spp. (bivalve: 11.4%), *Synodus luciocepis* (teleost: 5.8%), *Neverita lewisii* egg cases (gastropod: 5.1%), *Stylatula elongata* (anthozoan: 5.1%), infaunal Ophiuroidea (4.1%), *Adelgorgia phylloscellara* (gorgonian: 3.6%), and Cancrid crabs (2.4%). Of note, the gastropods *Kelletia kelletii* and *Neobernaya spadicea*, as well as the teleosts *Sebastes* spp. were not observed in association with embryo capsules.

Adults did not attach capsules on kelps near the NLJ site (Fig. 5), although observations were made of embryo capsules attached to kelp fronds outside of the forest (Navarro 2014). Notably, there was a precipitous decline of capsules observed near the edge of the kelp forest (Fig. 6). A 50-m-wide zone over the sand next to the kelp forest mainly lacked embryo capsules (Fig. 6). Within this area, capsules were observed only twice and were at the lowest densities of any of the areas observed at NLJ (0.09 capsules/m^2; Fig. 6B). The kelp edge habitat had similar chemical, physical, and geological properties as nearby embryo beds.

Other areas having similar physicochemical characteristics that were mainly unoccupied by squid embryos included areas where the sand dollar *Dendraster excentricus* was densely distributed (approximately thousands/m^2) and co-occurrence was rare (only 0.5% of all market squid capsules were observed in association with sand dollars). Furthermore, market squid capsules were only observed as single-isolated capsules, where they co-occurred with sand dollars.

Essential Embryo Habitat and Footprint through Year-Round Spawning

Market squid embryos occurred throughout all seasons from the summer of 2012 through the fall of 2013 as observed in

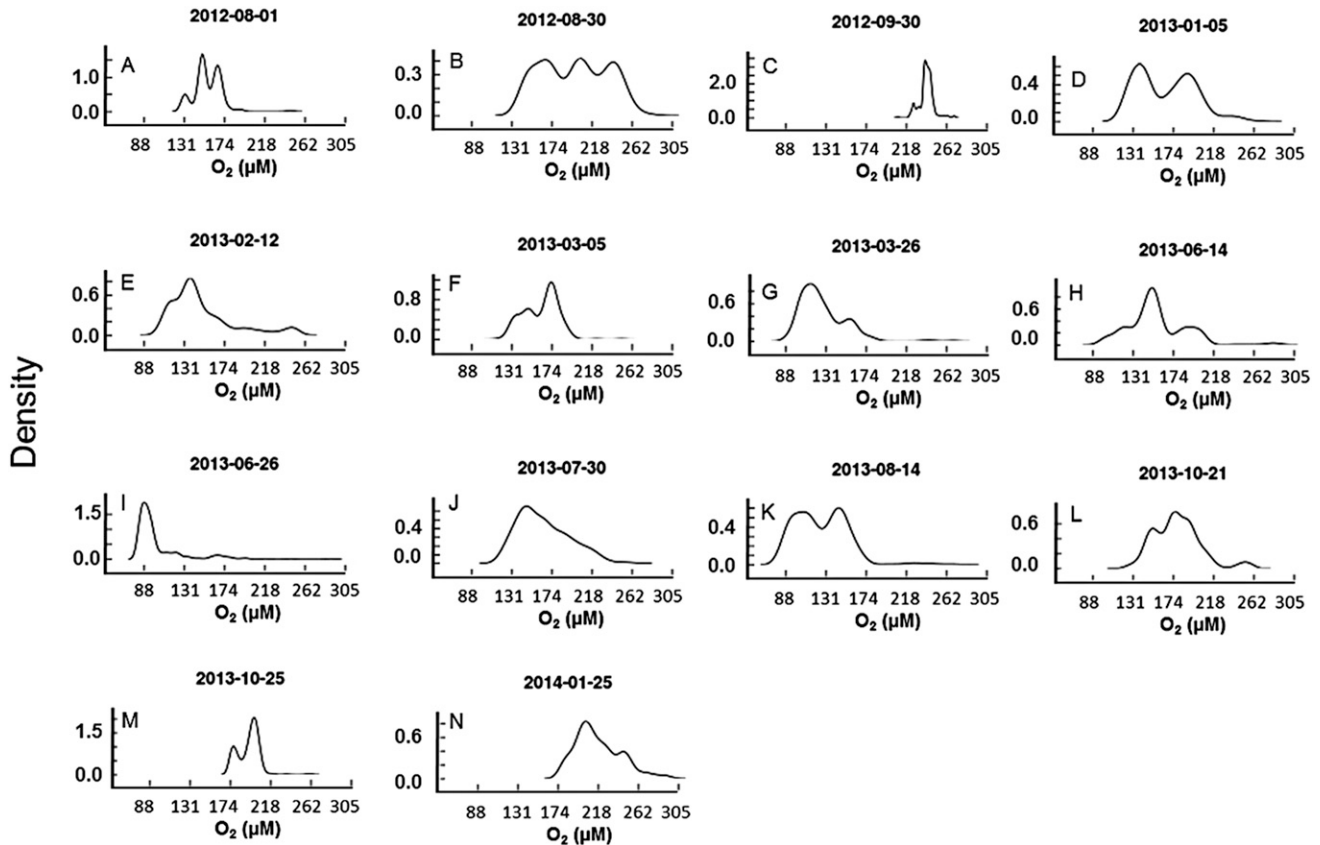**Figure 4. Probability density distributions of dissolved oxygen, μmol/kg (μM) per ROV survey date. (A). August 1, 2012. (B). August 30, 2012. (C). September 30, 2012. (D). January 5, 2013. (E). February 12, 2012. (F). March 5, 2013. (G). March 26, 2013. (H). June 14, 2013. (I). June 26, 2013. (J). July 30, 2013. (K). August 14, 2013. (L). October 21, 2013. (M). October 25, 2013. (N). January 25, 2014.**

the ROV surveys. Seasonal observations of capsules were fairly uniform (spring = 2, summer = 3, fall = 2, and winter = 3; see Tables 2 and 3). At NLJ, dying or dead spawning squid and empty capsules (indicating hatched embryos) were commonly observed. Embryo capsules were observed over large areas, where mass spawning occurred (Fig. 5).

DISCUSSION

This study provides the first direct evidence that market squid can spawn throughout the year in the SCB. Market squid were first observed to spawn year-round off Monterey, CA (Fields 1950). Previously in the SCB, year-round spawning had only been inferred from statolith-based age estimation (Jackson & Domeier 2003, Reiss et al. 2004). A recent genetic study provided molecular evidence supporting year-round spawning throughout regions of California and indicated that squid self-recruit to their natal regions ~66% of the time (Cheng 2015). Although self-recruitment was not tested, it is the most parsimonious explanation for the timing of squid spawning observed during the study. For many species, likely including market squid, embryo habitat site selection involves a mix of approaches from tradition-based to individual assessment (Warner 1990). Although this area of research is data poor for market squid, understanding how female squid select sites to deposit embryos, along the gradient from tradition to individual assessment, establishes a

foundation for understanding the environment that embryos experience in nature.

The spatial pattern of embryo deposition was clearly affected by variation in T, O_2, pH, and S, whereas the timing of spawning appears independent of abiotic factors. When shelf sites with high [O_2] and pH_T ([O_2] > 160 μmol, pH_T > 7.8, respectively) are limited to less than 40 m depth, squid typically restricted capsule deposition to the shallows (≤40 m depth) and in dense aggregations (>>2 capsules/m^2). Loliginid embryos are dependent on aerobic metabolism and can be negatively affected by low [O_2] (Roberts 2005, Zeidberg et al. 2011). By contrast, when the high [O_2] and pH zone expands to the 90-m contour, squid appear to respond by laying embryo capsules over a broader range of depths and at low densities effectively making them more cryptic. Crypsis is a primary defense strategy for cephalopods (Hanlon & Messenger 1996), therefore, embryos encompassing a larger area at lower density can potentially increase their survival. The observations of the prevalence of "cryptic" spawning events in this study are novel.

Squid embryo habitat is spatiotemporally dynamic because environmental conditions on the southern California shelf are highly variable. Internal waves are amplified near sharp topographic breaks, such as submarine canyons crests, where many persistent egg deposition sites are located immediately up-shelf, thus, enhancing physicochemical variability. All sessile organisms that inhabit the shelf, including market squid embryos, are exposed to oscillating physical conditions (frequency of 6–12 h)
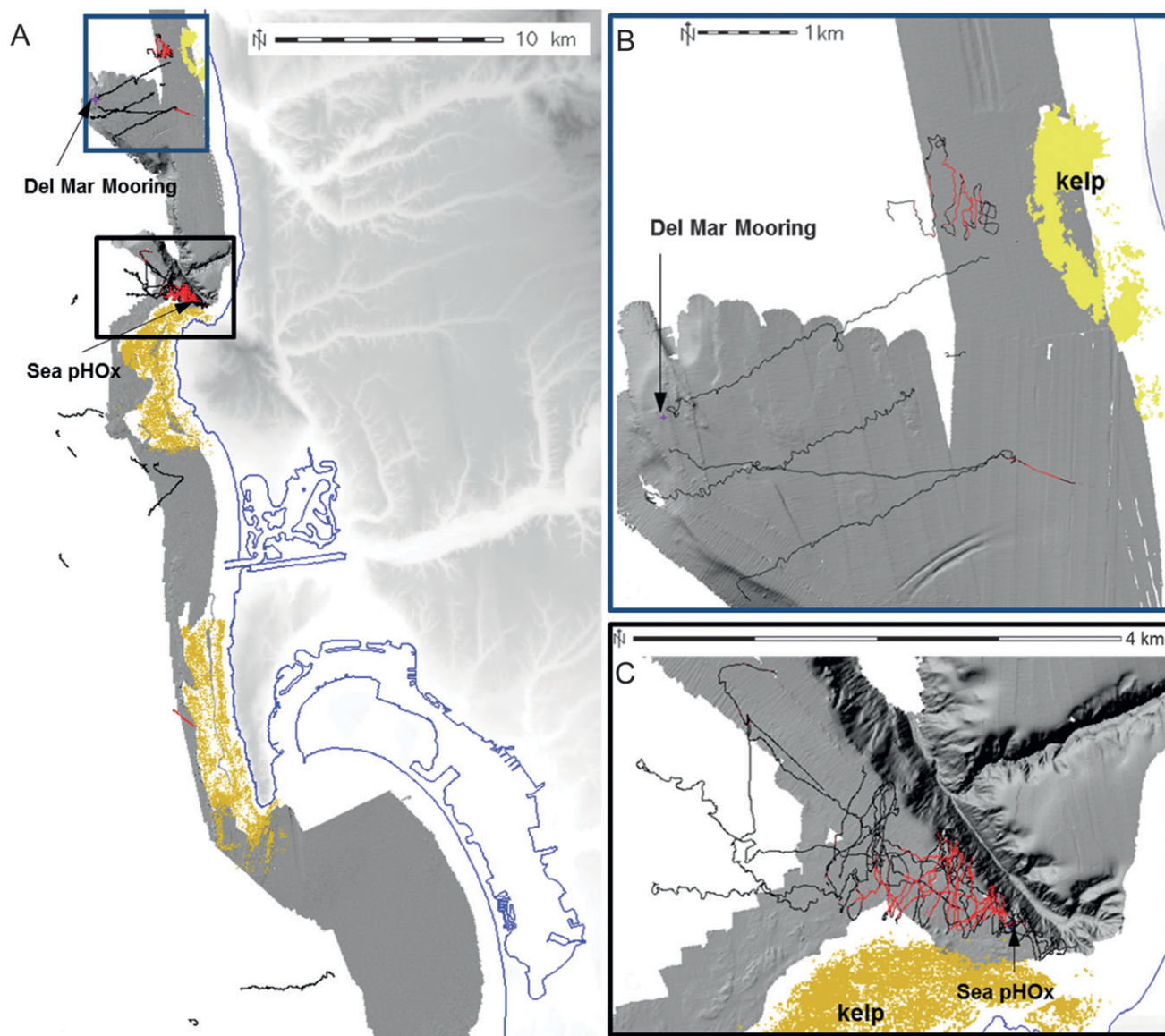
Figure 5. Remotely operated vehicle tracks indicating squid embryo presence (red) and absence (black) for all areas surveyed offshore of San Diego County, United States (A). Magnified view of the surveys conducted offshore of Solana Beach (B) and north La Jolla (C). Kelp is indicated in khaki.

due to internal tides and waves. Often, water masses with high $[O_2]$ and pH alternate with waters having low $[O_2]$ and pH driven by thermocline variation at daily to seasonal scales. Results of laboratory studies indicate that squid embryos can survive in low $[O_2]$ and pH environments (Navarro et al. 2016, Pierce 2017). Extended periods of low $[O_2]$ and pH are stressful to market squid embryos as evidenced by decreased hatch rates (Pierce 2017). A 2-wk period of upwelling in April 2013 when $[O_2]$ and pH were consistently low was observed (Fig. 9). Exposure to low pH and $[O_2]$ conditions will likely become increasingly frequent given predicted changes in the California Current System (Gruber et al. 2012). Chronic stressful exposures may occur most frequently during strong La Niñas [positive Southern Oscillation Index, negative Multivariate ENSO Index, and negative California Cooperative Oceanic Fisheries Investigation (CalCOFI) temperature anomaly] and during seasonal upwelling events (spring/summer), when the upwelling

index is sustained >200 m^{-3} s^{-1}/100 m coastline (Jackson & Domeier 2003, Nam et al. 2011, Send & Nam 2012). Local physicochemical climates are hypothesized to control optimal spawning habitat, and biotic interactions interact with these climates to affect realized spawning habitat.

Optimal Embryo Habitat and ENSO

The relationship between market squid and ENSO appears to vary among life stages. The results of this study indicate that market squid have much more suitable habitat available for egg deposition during El Niños because T, O_2, and pH through all depths down to ~100 m are conducive for embryo development (Table 3). Conversely, shelf conditions are stressful for squid embryos during La Niñas, (Navarro et al. 2016, Pierce 2017) when $[O_2]$ and pH are depressed (Nam et al. 2011, Turi et al. 2018). Depressed pH and $[O_2]$ environments slow embryo
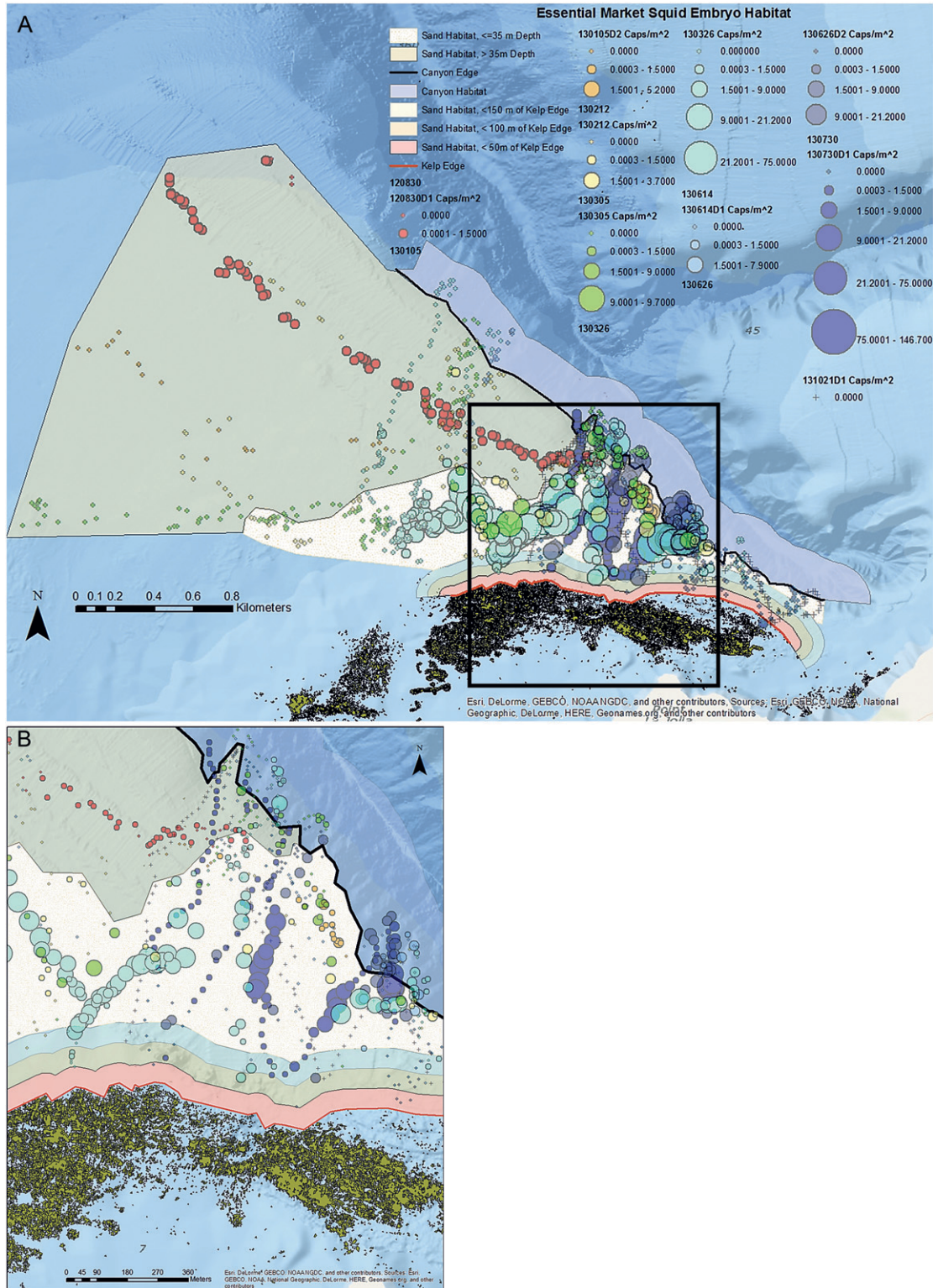
Figure 6. Bubble plot of squid capsules (capsules/m^2) observed among habitats for all ROV surveys at north La Jolla (NLJ) (A) and in relation to the canyon and kelp forest edges (B).

growth rates, leading to a longer embryo period, increase the frequency that embryos remained underdeveloped (Navarro et al. 2016), decrease hatch rates, and significantly alter gene expression of stress response in oxygen-sensitive genes and

transcriptome factors involved in developmental timing (Pierce 2017).

La Niña and other low [O$_2$] conditions are clearly unfavorable for developing embryos. There is recent evidence indicating that
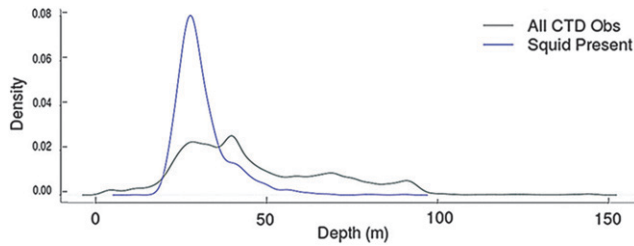
Figure 7. Probability density distributions of depth in ROV surveys, when embryo capsules were (blue) and were not (black) observed.

La Niña conditions are also adverse for the paralarval life stage (Perretti & Sedarat 2016). Predicted environmental conditions at the NLJ spawning site include increasing acidification (Gruber et al. 2012, Takeshita et al. 2015) that will likely coincide with reduced oxygenation and warming (Turi et al. 2018). As periods of low oxygen and pH exposure increase in frequency and intensity, market squid embryo habitat will likely be compressed in time and space, and the occurrence of large and dense spawning aggregations may become increasingly frequent. It is presently impossible to gauge the relative importance of mass deposition and cryptic deposition on squid population dynamics.

Biotic Control as a Driver of Realized-Embryo Habitat

Biotic interactions appear to be an important factor for spawning site selection. Site selection affects the ability of embryo capsules to remain anchored to the substrate long enough for development. Such biological factors interact to define the realized habitat of market squid and are essential for an accurate understanding of embryo environmental exposure climates.

Adults may aggregate for defense, to overwhelm marine mammals and other predators when embryo habitat is compressed. Aggregated spawning has likely evolved to satiate predators, enabling an adequate number of spawning squid to

mate and lay eggs. In this study, predation might influence spawning site selection for embryo deposition. Embryo capsules were rarely observed within the 50-m boundary adjacent to kelp forests, both off La Jolla and Solana Beach. Areas adjacent to kelp forests are hypothesized to represent a potential "zone of fear" or an area with enhanced predation of spawning squid, and represent a biotic control of squid embryo habitat. Predators of squid (e.g., fish) are abundant within and at the edges of kelp forests. During this study, squid embryo capsules were rarely observed within sand dollar beds. Avoidance of kelp forests and their edges, and the avoidance of sand dollar beds clearly limit embryo depositional habitat.

Possible predatory controls on embryo bed distribution most commonly found in kelp beds include *Kelletia kelletii*, *Neobernaya spadicea* (Zeidberg et al. 2004), and *Sebastes* spp. (Zeidberg et al. 2011). In this study, observations of biota found with squid embryo capsules differ from a report from Monterey Bay, which includes *Patiria miniata*, *Mediaster aequalis*, *Pycnopodia helianthoides*, *Citharichthys stigmaeus*, and *Rhinogobiops nicholsii* (Zeidberg et al. 2004).

Observations of squid commonly using submarine canyon walls as embryo habitat have not been reported previously (Young et al. 2011). The lack of reporting may be an artifact that reflects difficulties encountered in complex geological areas, where ROV and AUV observations are problematic. The distributions of embryo capsules observed in this study support the premise that predation pressure on spawning squid dictates the realized embryo habitat pattern rather than predation on embryos themselves.

Identifying the Population Bottleneck and Resolving the ENSO Paradox

For more than a decade, scientists have questioned why market squid spawning is depressed when environmental conditions (El Niños) are favorable for embryo development and growth. Jackson and Domeier (2003) found that squid grow faster at warmer temperatures, yet, in nature, adult squid are

TABLE 2.

Spatial surveys (ROV): summary data.

Survey number	Date	Season	ROV coordinates	Location	Survey depth range (m)	*Doryteuthis opalescens* embryo depth range (m)
1	August 1, 2012	Summer	32.80° N, 117.31° W	Pacific Beach	38.2–75.1	Absent
2	August 30, 2012	Summer	32.86° N, 117.28° W	NLJ	33.4–91.5	33.4–91.5
3	August 30, 2012	Summer	32.93° N, 117.30° W	Del Mar	40.6–94.4	Absent
4	September 30, 2012	Fall	32.95° N, 117.28° W	Solana Beach	22.0–40.0	22.0–40.0
5	January 5, 2013	Winter	32.86° N, 117.28° W	NLJ	28.5–71.0	28.5–33.4
6	January 5, 2013	Winter	32.80° N, 117.31° W	Pacific Beach	39.9–70.8	Absent
7	February 12, 2013	Winter	32.86° N, 117.28° W	7 NLJ	11.2–65.1	11.3–55.3
8	March 5, 2013	Winter	32.86° N, 117.28° W	8 NLJ	21.0–77.4	24.7–64.1
9	March 26, 2013	Spring	32.86° N, 117.28° W	NLJ	19.0–78.9	21.2–68.4
10	June 14, 2013	Spring	32.86° N, 117.28° W	NLJ	16.1–75.9	21.6–40.6
11	June 26, 2013	Summer	32.86° N, 117.28° W	NLJ	13.2–74.8	24.9–48.3
12	June 26, 2013	Summer	32.80° N, 117.31° W	Pacific Beach	19.6–80.3	Absent
13	July 30, 2013	Summer	32.86° N, 117.28° W	NLJ	11.2–82.8	10.3–65.5
14	July 30, 2013	Summer	32.70° N, 117.27° W	Point Loma	31.2–50.5	31.2–50.5
15	August 14, 2013	Summer	32.93° N, 117.30° W	Del Mar	23.9–93.8	Absent
16	October 21, 2013	Fall	32.86° N, 117.28° W	NLJ	6.2–103.1	Absent
17	October 21, 2013	Fall	32.93° N, 117.30° W	Del Mar	8.8–126.1	23.1–40.2
18	January 25, 2014	Winter	32.93° N, 117.32° W	Del Mar	36.5–146.5	Absent

TABLE 3.

Estimated total embryo count per ROV survey.

Survey number	Max [O_2] (μM)	Max pH	O_2/pH max zone depth (m)	Squid max density depth (m)	Squid max density (capsules/m^2)	Squid average density (capsules/m^2)	Estimated bed area (m^2)	Estimated embryo/ capsule	Estimated total embryo count
2	250.3–266.3	8.00–8.06	33.4–43.1	42.0	1.5	0.063	569,720	129	4,630,114
4	250.6–276.9	8.03–8.11	12.5–32.0	28.1	350.1	7.919	516,852	128	523,897,726
5	190.3–194.2	7.88–7.89	28.5–38.2	29.2	5.2	1.548	15,494	141	3,381,844
7	254.8	8.01	11.3–29.7	28.7	3.7	0.158	294,949	153	7,130,097
8	185.3–199.1	7.86–7.89	21.0–34.8	29.2	9.7	0.267	371,430	162	16,065,833
9	160.2–184.0	7.81–7.86	26.6–31.2	27.9	71.4	3.714	731,642	171	464,661,444
10	202.6–212.5	7.89–7.90	19.1–26.1	28.0	7.9	0.183	78,494	219	3,145,804
11	169.7–182.4	7.83–7.88	13.3–19.4	27.8	21.2	1.859	193,653	227	81,720,210
13, 14	204.6–239.6	7.90–7.98	10.3–22.5	24.9	146.7	4.365	317,686	254	352,221,645
17	198.7–214.8	7.86–7.90	23.1–39.4	35.9	0.224	0.086	42,640	249	913,093

The depth range where squid-embryo densities were highest closely tracked the inner-shelf depth where O_2 and pH levels were at their maximums, respectively.

larger during cold years such as La Niña (Lowry & Carretta 1999, Brady 2008). Not only are squid larger, but also many report a higher abundance of squid during La Niña (Vojkovich 1998, Reiss et al. 2004, Koslow & Allen 2011, Dorval et al. 2013, Van Noord & Dorval 2017). Jackson and Domeier (2003) explained this paradox suggesting that the market squid population must go through a population bottleneck. They inferred that a lack of food was responsible and that the juvenile stage was the most likely stage for bottlenecks to occur. Jackson and Domeier (2003) made this inference based on evidence that large squid were associated with upwelling environments during their early life stages. They posited that upwelling increased food supplies for growing juveniles. By contrast, adults inhabiting areas with little upwelling grew to smaller sizes (Jackson & Domeier 2003). Jackson and Domeier (2003) did not test their bottleneck hypothesis for any squid life stages. Perretti and Sedarat (2016) investigated the paralarval bottleneck hypothesis

Figure 8. Probability density distribution comparisons of depth (A) and oxygen (B) with two distinct squid capsule aggregation types, "few" ($\leq$5 capsules/m^2, black) and "abundant" ($\geq$25 m^{-2}, blue). The arrow highlights high density of observations of abundant, compared with the "few" classification, when dissolved oxygen was low.

using field samples collected by the CalCOFI. They found that paralarvae, standardized by age, were larger during El Niño than they were during La Niña, providing no evidence of population bottlenecks at the paralarval stage (Perretti & Sedarat 2016). Instead, Perretti and Sedarat (2016) proposed that juvenile squid experience a bottleneck due to food limitation associated with El Niño. Van Noord and Dorval (2017) proposed that market squid recruit to the fishery in the highest numbers when the timing of juveniles matches periods with the highest concentrations of euphausiids, typically in spring. Sampling both juvenile squid and their prey may shed light on the interacting effects of oceanographic factors and trophic pathways (Ralston et al. 2018). A recent increase in commercial squid catch in California (CDFG preliminary report) coincides with increased upwelling in the SCB (Wells et al. 2017), supporting these hypotheses.

Another factor that is problematic for determining the occurrence of population bottlenecks is that field sampling methods likely introduce significant temporal bias. As such, interpreting data is often difficult. For example, in this study, squid capsules varied greatly in density and areal coverage making most spawning events cryptic to the fishery, and potentially to classical sampling techniques. Data from aging studies and this study indicate that squid spawn and hatch in the SCB every month (Jackson & Domeier 2003, Reiss et al. 2004). Yet, studies of spawning squid and paralarvae focus on periods when squid form dense aggregations (and lay dense embryo capsules which lead to dense paralarvae), potentially, introducing an aggregation bias in sampling methods that is difficult to eliminate. Previously, researchers attempting to understand sampling error by relating paralarval and embryo abundances strongly cautioned that paralarval sampling should not be analyzed quantitatively (Okutani & McGowan 1969). Researchers also have found that areas with high squid paralarval densities did not coincide with areas having abundant zooplankton (Okutani & McGowan 1969, Van Noord & Dorval 2017). Okutani and McGowan (1969) also suggested that squid abundance is not adequately sampled by CalCOFI because nets are designed to catch fish, not squid (Okutani & McGowan 1969). Other authors have gone further and suggested that CalCOFI sampling of paralarvae offshore may not
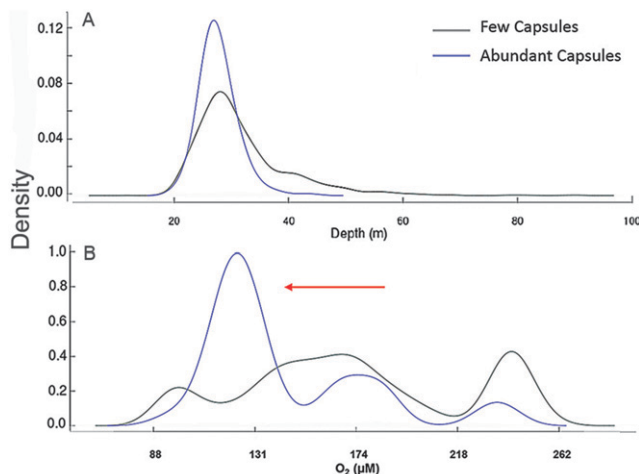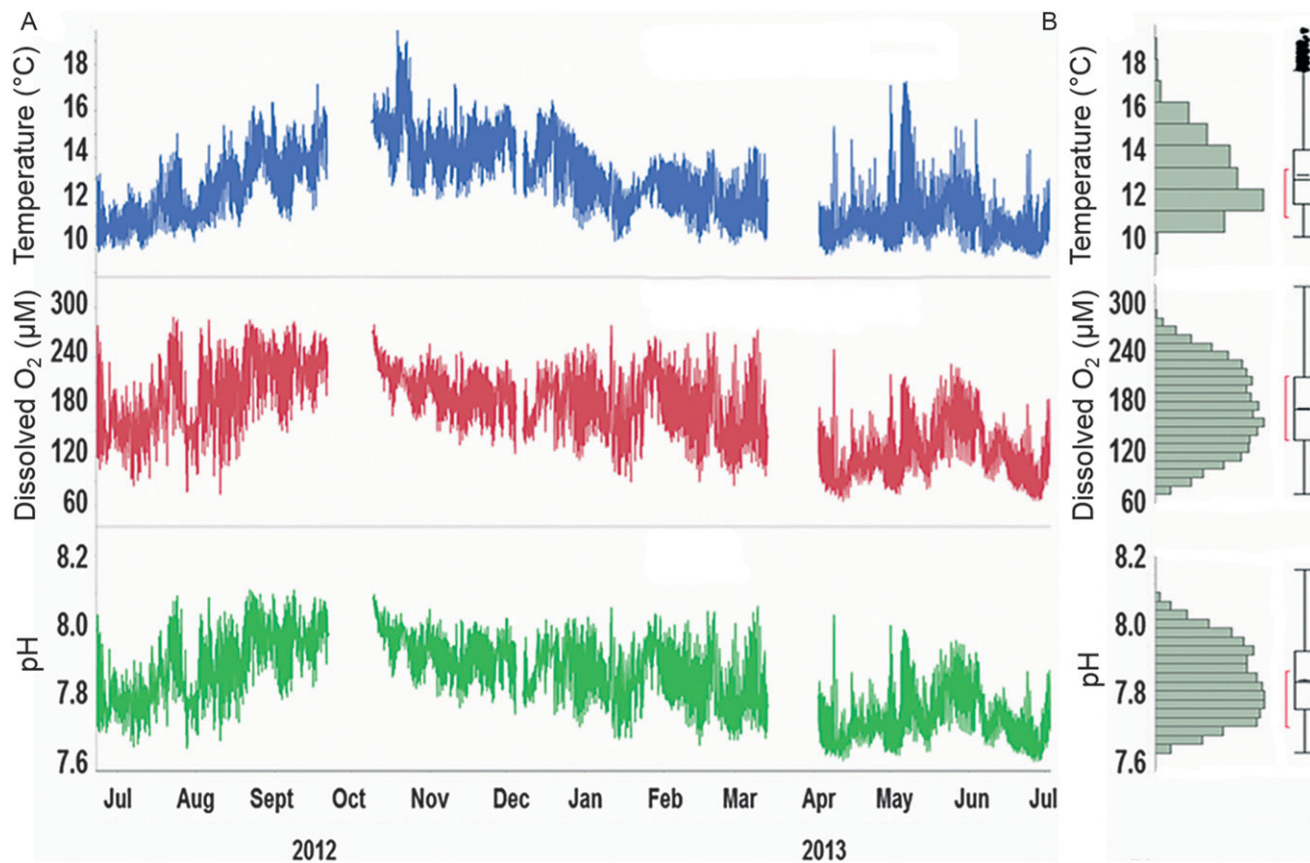
Figure 9. SeapHOx data at the fixed north La Jolla site (30 m deep). Temperature, dissolved oxygen and pH data from June 2012 to July 2013 (A). Histograms of temperature, dissolved oxygen and pH (B).

provide an accurate proxy for assessing squid interannual abundance (Zeidberg & Hamner 2002).

This study demonstrates how market squid can change their behavior within a spawning site. Also, market squid can also migrate among spawning sites, likely following prey, when El Niño affects coastal water mass distributions (Bernard 1980, Street 1983, Wing & Mercer 1990). During these time periods, market squid more heavily use spawning sites in the northern parts of their range. These include sandy subtidal regions of Northern California, Oregon (Jefferts et al. 1987), Washington, Vancouver Island (Shimek et al. 1984), the central coast of Canada (Bernard 1980), and Southeast Alaska (Wing & Mercer 1990). Egg capsules were reported in the Gulf of Alaska, near Kodiak Island in 2016 (Foy, personal communication). The spatial scale of study should encompass the geographic range of their embryo sites to understand the among-site dynamics along with those within a site.

Sampling has been improved with more recent assessments that focus on nearshore CalCOFI stations and manta tows (unbridled net; Koslow & Allen 2011). A recent development uses increased spatiotemporal paralarval surveys designed *a priori* to target and catch squid (Van Noord & Dorval 2017) and juvenile data sets are beginning to emerge (Ralston et al. 2018). Yet, future research may still benefit by comparing squid sampling methods to improve the scientific understanding of their precision, accuracy and associated error. For any given life stage, methods are needed that account for (1) spatiotemporal patchiness (especially within and among embryo habitat sites), (2) highly variable densities and

abundances, and (3) behavioral plasticity within pelagic and benthic habitats. Of the mobile stages, the juvenile stage is the most data poor but may also be the most important to understand market squid population bottlenecks.

Improving Abundance Estimation

The "illusion of plenty" represents an error that occurs when assessing aggregated spawning populations (Erisman et al. 2011). Large aggregations of spawning market squid are often cited as an indicator of a large population size when, in reality, it may be more reflective of a population that is displaced in response to habitat compression. Without reliable biomass estimates and knowledge of nonspawning adult distributions (Cheng 2015), it is difficult to know the magnitude at which population abundances are changing relative to the magnitude that population distributions are changing. Of note, high O_2 and pH zones may have been limiting in the early 1950s (CalCOFI Archives, McClatchie et al. 2010) when the total abundance estimate for squid embryos was 1.76×10^{12} (Okutani & McGowan 1969). This estimate is three orders of magnitude larger than the largest measured abundance of 5.23×10^{9} in this study (Table 3). Furthermore, densities reported before the development of the mature fishery were as high as 10,400 embryo capsule/m^2 (Okutani & McGowan 1969). Density counts in SCB in 2001 to 2002 were reported as high as 1,338 capsules/m^2 (Zeidberg et al. 2011). This study reports densities as high as 350 embryo capsules/m^2. Heavy fishing pressure
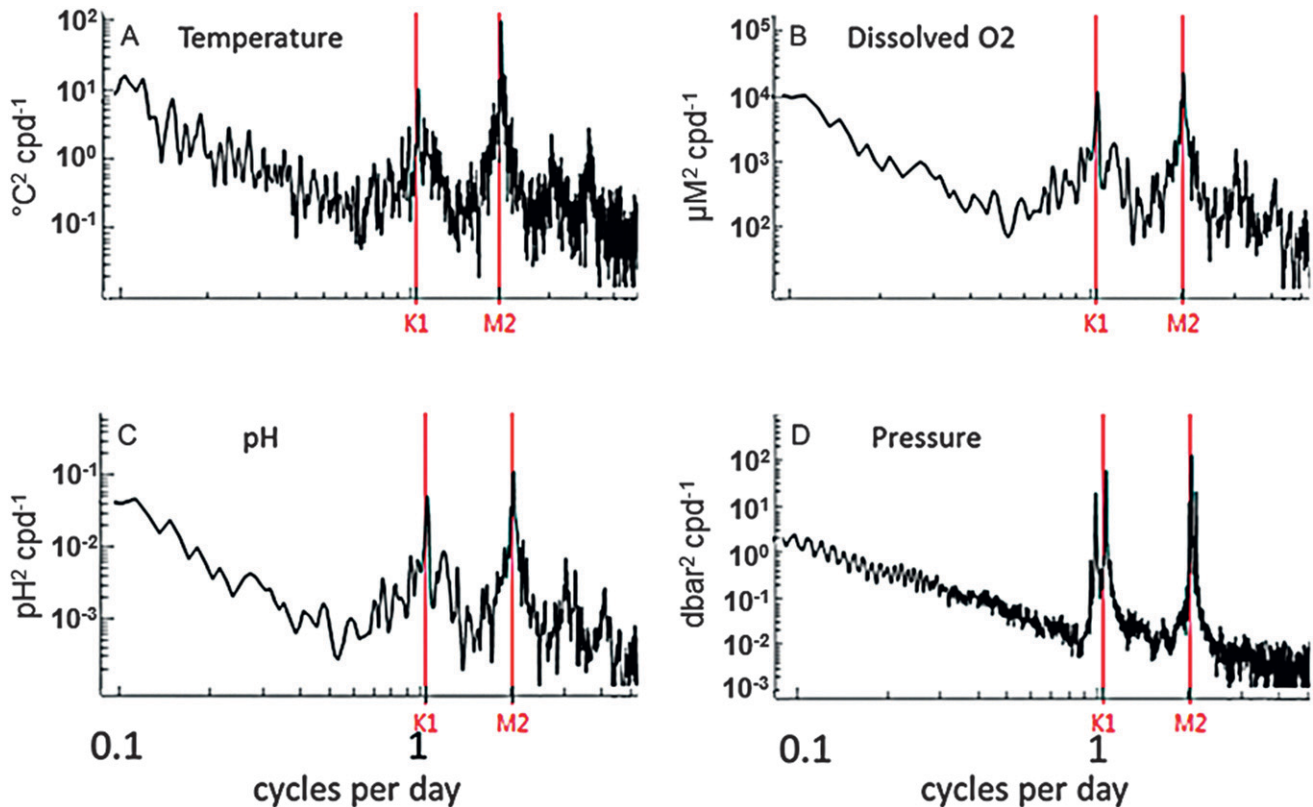
Figure 10. Spectral densities of temperature (A), dissolved oxygen (B), pH (C), and pressure (D). Red lines indicate K1 and M2 frequency tidal cycles.

can lead to less egg deposition despite high spawning biomass (Moltschaniwskyj & Pecl 2007). Potential ecological effects of overfishing this keystone species are great because squid bring nutrients and energy from the slope to the shelf. Reductions in their numbers could alter food webs and energy budgets for many species (Morejohn et al. 1978, Lowry & Carretta 1999).

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