



Taxonomic composition, abundance and habitat associations of squid paralarvae in the northern Gulf of Mexico

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ABSTRACT

Summer plankton surveys were conducted in 2015–2017 to characterize the distribution and abundance of squid paralarvae in epipelagic waters of the northern Gulf of Mexico (Gulf). Paralarvae present at stations sampled were from 12 families, with the most abundant being Ommastrephidae (flying squids), Enoploteuthidae (armed squids) and Onychoteuthidae (hooked squids). Mean density and percent frequency of occurrence for squid paralarvae across all surveys was 8.8 paralarvae 1000 m⁻³ and 76%, respectively. Julian day, salinity, sea surface height (SSH) and time of day were identified as influential environmental variables in generalized additive models (GAMs). Paralarval densities peaked during early morning and late evening sampling times, which is in accord with diel vertical migration patterns. Densities increased in early July, in areas with low SSH and lower salinity (28–35 psu), indicating upwelling areas and proximity to inflow from the Mississippi River represent productive early life habitats for squid. Results suggest that oceanic squid spawn in the northern Gulf in the summer exploiting the position of mesoscale oceanographic features and the extension of freshwater discharges from the Mississippi River.

1. Introduction

Pelagic cephalopods, primarily squids, are dominant prey for several marine organisms, including migratory pelagic fishes (i.e. billfishes, tunas, and sharks), sea birds, and marine mammals (Clarke, 1996; Logan et al., 2013; Rodhouse et al., 2013; Staudinger et al., 2013). Squids are voracious predators as well and are essential components in open-ocean food webs, transforming biomass of micronekton into high-energy food for large predators (Clarke, 1996). It has been estimated that the yearly consumption of squids by sperm whales alone is greater than the total world catch of all marine and freshwater organisms combined (Clarke, 1977, as cited in Hoving et al., 2014). Squids occupy a large range of trophic levels, even exhibiting significant top-down control on their prey; however, as an important prey to large pelagic predators, open-ocean squids are constrained to a bottom-up control on their predators and can be regarded as keystone species in pelagic ecosystems

(Coll et al., 2013). In fact, squid populations are increasing as predation and competition is reduced due to overexploited fish stocks (Caddy and Rodhouse, 1998).

Squids grow rapidly, have short lifespans (usually <2 years), and are semelparous, resulting in a fast life-history strategy (O'Dor and Webber, 1986). While this life strategy allows squids to be opportunists and take advantage of favorable environmental conditions, sudden deterioration of the environment or food sources can cause rapid declines in abundance and result in pronounced interannual variation in population sizes (Rodhouse et al., 2014). Despite these fluctuations, recent studies suggest that cephalopod populations are steadily increasing over time due to oceanic environmental changes (Doubleday et al., 2016). Still, cephalopod population dynamics are poorly understood and difficult to forecast due to their adaptability to changing conditions and opportunistic life history traits (Rodhouse et al., 2014; Doubleday et al., 2016). An improved understanding of squid abundance and habitat

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associations based on environmental factors during the pelagic paralarval stage is critical to population modeling efforts because recruitment variability is commonly linked to early life events (Cowen et al., 2000).

Little is known about the early life ecology of pelagic squids in the northern Gulf of Mexico (Gulf), which is a region that maintains some of the most productive fisheries in the United States (Chesney et al., 2000). The influences of the Mississippi River and mesoscale features, such as the Loop Current and associated eddies, provide nutrient rich habitats that increase primary and secondary production (Govoni et al., 1989; Biggs, 1992). Further, the northern Gulf is also recognized as an important spawning and nursery habitat for several large pelagic predators that are known to feed heavily on cephalopods, including billfishes, tunas, and cetaceans (Rooker et al., 2012; Ruiz-Cooley et al., 2012; Kitchens and Rooker, 2014; Judkins et al., 2013; Cornic et al., 2018). The purpose of the present study is to use a generalized additive modeling framework to characterize early life habitats of squids and to identify influential environmental parameters that affect their relative abundance and distribution in this basin.

2. Material and methods

2.1. Sample collection

Squid paralarvae were collected during annual plankton surveys conducted in shelf, slope, and open-ocean stations of the northern Gulf from approximately 27.0 to 28.0°N latitude and 88.0 to 91.0°W longitude. The 48 sampling stations were divided between two transects at 27.0°N and 28.0°N, with stations spaced approximately 15 km apart along each transect (Fig. 1). Plankton surveys have been conducted in this region from 2005 to 2017 due to its proximity to the Mississippi River, the northwestern margin of the Loop Current and associated eddies, as well as including open-ocean sites (Kitchens and Rooker,

2014; Randall et al., 2015; Cornic et al., 2018). In the summers of 2015 and 2016, two surveys were conducted each year (early June and late July) during daylight hours (0600–2000 h). The 2016 early June survey ended abruptly due to inclement weather and resumed from 6/30/2016 to 7/1/2016. The delay of the 2016 early June survey to early July resulted in an increase of squid paralarvae collected, even though fewer stations were sampled (38 of 48). Thus, it was decided to add an additional early July survey in 2017 to increase samples of paralarvae.

Paired bongo nets (frame 61 cm, mesh sizes 333 μm and 500 μm) were deployed at each station within the sampling area. The oblique bongo net tows were conducted to a depth of 100 m at a tow speed of 2.5 knots, lasting approximately 10 min. Flowmeters (General Oceanics Model, 2030R, Miami, FL) were affixed to the center of each net to determine the volume of water sampled during each tow. Density of squid paralarvae at each station was expressed as the number of paralarvae 1000 m^{-3} of water volume sampled and based on combined catches between the paired bongo nets. The entire contents of each of the cod ends were fixed onboard in 95% ethanol for transport to the laboratory.

Sea surface temperature (SST, °C), salinity (psu), and dissolved oxygen (DO, mg L^{-1}), were recorded at each station using a Sonde 6920 Environmental Monitoring System (YSI Inc.). Sea surface height (SSH, m) was obtained from Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu/>) based on satellite altimetry measurements (MULTIOBS_GLD_PHY_NRT_015_001) calculated weekly at a resolution of 0.25°. Distance to the Loop Current was estimated by measuring the linear distance from the edge of the feature (based on the contour extracted from the SSH raster) to each sampling station using the Vector General toolbox in QGIS v3.10. Water depth (m) at all sampling stations was extracted from GEODAS U.S. Coastal Relief Model with 3 arc-second grids (www.ngdc.noaa.gov).

Squid paralarvae were sorted from the plankton samples in the



Fig. 1. Survey stations (black dots) in the northern Gulf of Mexico where squid paralarvae collections occurred in 2015–2017. The blue lines represent depth (m) contours. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

laboratory under a Leica MZ stereomicroscope and preserved in individual vials that contained 70% ethanol. Squid samples were then identified visually to family level based on morphometric and anatomical features. Identification to species level was determined when possible (Supplementary Table S1). As most paralarvae could not be identified confidently to the genus and species level, results were compiled and calculated at the family level. Mantle length (ML, mm) was recorded, when possible, for each individual.

2.2. Statistical analysis

Generalized additive models (GAMs) were used to determine the influence of environmental parameters on paralarval squid density. Paralarval abundance at each station was calculated using pooled squid counts between the 333 μm and 500 μm mesh nets and was modeled as the response variable. A natural logarithm transformation of the volume of water surveyed at each station (combined between the two nets) was included as an offset variable to account for effort. Negative binomial models were developed using the 'mgcv' library (Wood, 2006) for R software packages (R Core Team 2014), with cubic splines restricted to three degrees of freedom (df) to prevent overfitting and unrealistic ecological responses (Ciannelli et al., 2008; Furey and Rooker, 2013; Dance and Rooker, 2016). Density of all squid paralarvae was modeled against environmental variables over the three-year period (2015–2017). Additional GAM models were developed for the most abundant squid families (Ommastrephidae, Enoploteuthidae, and Onychoteuthidae) collected. Explanatory variables used in GAMs included oceanographic (SSH, water depth, and distance to the Loop Current), physical and chemical (SST, salinity, and DO), and temporal (Julian day, time of day, and year) variables.

A manual backwards stepwise procedure was used to select explanatory variables influencing paralarval squid density based on minimizing the Akaike Information Criterion (AIC; Akaike, 1974). During each step of the backwards selection process, the variable with the highest p-value ($p > 0.05$) was removed until the lowest AIC was achieved, resulting in the model with the best fit. If the removal of a variable resulted in an increased AIC value, the variable was retained in the model and the backwards selection process was stopped. Percent deviance explained (DE) was calculated for each model to examine overall fit. Prior to running GAMs, tests for collinearity were performed using Spearman's correlation analysis. A high level of collinearity ($\rho > 0.70$) existed between Julian day and SST. The influence of both variables was tested alone in separate GAMs, with Julian day resulting in a lower AIC value and was allowed to enter the initial model before backwards stepwise selection. Once SST was removed from the model, low levels of collinearity existed among variables ($\rho < 0.50$). Upon selection of the final model, each remaining explanatory variable was removed individually from the final model to determine the relative importance of each variable based on ΔAIC and ΔDE (Rooker et al., 2012; Kitchens and Rooker, 2014).

3. Results

A total of 613 squid paralarvae was collected over the three-year sampling period, encompassing 12 families (Table 1). The majority were small, with an average ML of 2.4 mm.

(± 2.2 mm SD). Due to small size (< 1.5 mm ML) or damage from the net, 288 squid paralarvae could not be visually identified to family level. The most abundant family was Ommastrephidae with 108 individuals, accounting for 33% of paralarvae identifiable to family level for all three years combined. The next most abundant families were Enoploteuthidae ($n = 79$; 24% overall identifiable paralarvae) and Onychoteuthidae ($n = 52$; 16% overall identifiable paralarvae). Mean density of squid paralarvae per survey ranged from 3.5 (± 0.6 SE; 2015 early June) to 17.1 (± 1.4 SE; 2016 early July) individuals 1000 m^{-3} (Table 2). The maximum density of squid paralarvae detected at a single

Table 1

Catch data of squid paralarvae by families collected in 2015–2017 in the northern Gulf of Mexico (Mantle length = ML).

Family	Count (N)			% of Identifiable Paralarvae	Size Range (ML, mm)
	2015	2016	2017		
UNIDENTIFIED	58	107	123	–	0.5–4.8
<i>Squid</i>					
Ommastrephidae	33	58	17	33.2	0.5–7.5
Enoploteuthidae	23	41	15	24.3	1–8
Onychoteuthidae	25	7	20	16.0	1.5–5.5
Cranchiidae	2	4	13	5.8	1–25
Lycoteuthidae	3	8	8	5.8	1.5–4
Cycloteuthidae	5	6	5	4.9	1–3.5
Pyroteuthidae	3	5	3	3.4	1.5–4
Octopoteuthidae	2	3	5	3.1	1.1–9
Chiroteuthidae	0	1	3	1.2	2–4
Thysanoteuthidae	3	0	1	1.2	3–9.5
Ancistrocheiridae	0	0	2	0.6	3–3.5
Sepiolidae	0	0	1	0.3	2.5

station was 55 individuals 1000 m^{-3} during the 2016 early July survey. The mean density of ommastrephid paralarvae per survey ranged from 0.7 (± 0.6 SE; 2015 early June) to 5.2 (± 1.3 SE; 2016 early July) individuals 1000 m^{-3} (Table 2). Mean density of enoploteuthid paralarvae per survey ranged from 0.4 (± 0.8 SE; 2016 early June) to 3.4 (± 0.8 SE; 2016 early July) individuals 1000 m^{-3} , and onychoteuthid paralarvae ranged from 0.2 (± 0.5 ; 2016 early July) to 1.3 (± 0.5 SE; 2015 late July) individuals 1000 m^{-3} (Table 2).

Over the duration of the three-year study period, squid paralarvae (all taxa) were present at every station sampled (Fig. 2). Percent frequency of occurrence per survey (based on presence at stations sampled) of squid paralarvae was 52.1% for 2015 early June, 81.3% for 2015 late July, 71.4% for 2016 early June, 91.7% for 2016 early July, 72.9% for 2016 late July and 91.5% for 2017 early July (Table 2). Paralarvae from the most commonly encountered family (Ommastrephidae) were present in 14.6% (2015 early June) to 54.2% (2016 early July) of the stations sampled. Enoploteuthid paralarvae were present in 14.3% (2016 early June) to 58.3% (2016 early July) of the stations sampled, and onychoteuthid paralarvae were present in 6.3% (2015 early June and 2016 late July) to 27.7% (2017 early July) of the station sampled (Table 2).

The final GAM examining the influence of environmental variables on the density of all squid paralarvae had an AIC of 880.0 with 29.1% DE (Table 3). Variables retained in the model in order of significance, based on higher ΔAIC , were Julian day (46.4), salinity (11.5), SSH (8.5), and time of day (6.2). The ΔDE was also used to assess the influence of the variables on squid density, and the relative contribution was similar (Table 3). All factors were significant ($p < 0.05$). Response curves from the GAM revealed that paralarval density increased toward the middle of the sampling period, peaking at Julian day 185 (July; Fig. 3). Paralarval density was also greater in areas where salinity ranged from 28 to 35 psu, lower SSH (< 0.5 m), and during the early morning or evening hours.

The ommastrephid paralarval density final GAM had an AIC of 388.8 with 17.2% DE (Table 3). Influential variables retained in the model, with associated ΔAIC , were water depth (17.5) and distance to the Loop Current (13.4). Both factors were highly significant ($p < 0.001$). The ommastrephid model differed from the overall squid model by not retaining the same variables. Instead, response curves from the model indicated that ommastrephid density decreased at stations with increasing water column depth (< 2300 m) and increased at stations closer to the Loop Current (Fig. 4).

The final GAM based on the density of enoploteuthid paralarvae had an AIC of 327.9 with 16.6% DE (Table 3). Influential variables retained in the model, in order of significance based on higher ΔAIC , were distance to the Loop Current (10.3), SSH (5.6), and factor year (2.3).

Table 2

Summary of the count (N), density (paralarvae 1000 m⁻³) and percent frequency of occurrence (percent of stations paralarvae were found) for all squid and the dominant families collected during each survey in the northern Gulf of Mexico.

Survey	All Squid			Ommastrephidae			Enoploteuthidae			Onychoteuthidae		
	N	Density	% Freq	N	Density	% Freq	N	Density	% Freq	N	Density	% Freq
2015 Early June (June 6–9)	45	3.5	52.1	9	0.7	14.6	10	0.8	20.8	3	0.3	6.3
2015 Late July (July 20–25)	112	7.1	81.3	24	1.6	35.4	13	0.7	25	22	1.3	27.1
2016 Early June (June 9–10) ^a	26	6	71.4	7	1.6	35.7	2	0.4	14.3	2	0.5	7.1
2016 Early July (June 30–July 1) ^a	117	17.1	91.7	35	5.2	54.2	23	3.4	58.3	2	0.2	8.3
2016 Late July (July 23–28)	97	9.8	72.9	16	1.5	18.8	16	1.7	25	3	0.3	6.3
2017 Early July (July 1–4)	216	11.6	91.5	17	0.9	25.5	15	0.8	25.5	20	1.1	27.7
Overall	613	8.8	76	108	1.6	27.5	79	1.2	27.1	52	0.7	15.3

^a Inclement weather caused a delay during this survey; southern stations were sampled in early June and northern stations in early July.

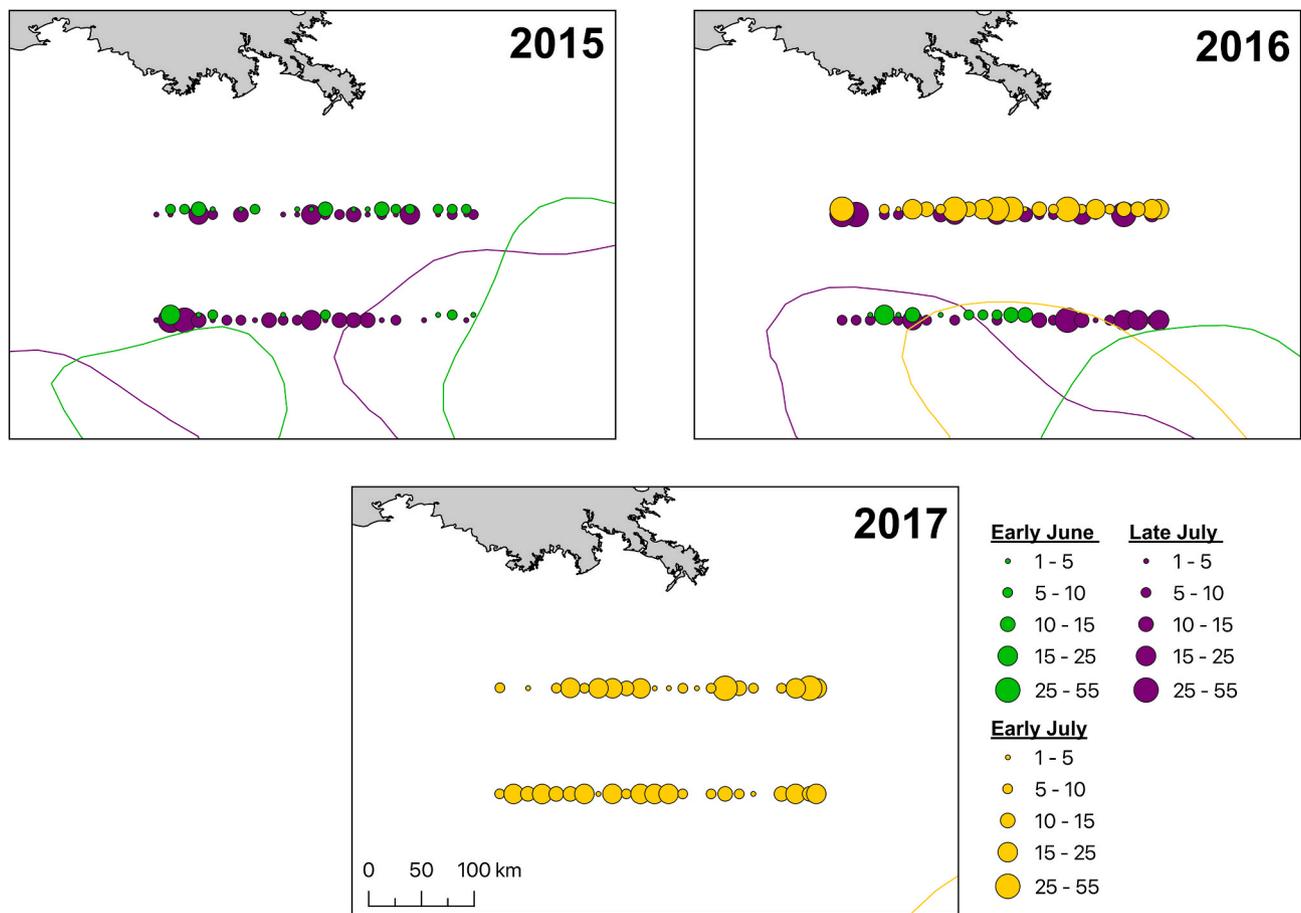


Fig. 2. Spatial and temporal (year) variability in density of squid paralarvae collected in 2015–2017 from plankton surveys in the northern Gulf of Mexico. Circle size indicates density when collected in early June (green), early July (yellow) and late July (purple), when applicable. Corresponding colored lines represent the Loop Current and potential eddies during sampling trips. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Similar to the overall squid model, response plots from the enoploteuthid paralarval density GAM showed an increase at lower SSH (<0.5 m; Fig. 5). The enoploteuthid model was also similar to the ommastrephid model by including distance to the Loop Current, indicating that enoploteuthid density increased as distance to the Loop Current decreased (Fig. 5). Enoploteuthid paralarval density was highest in 2016. However, as distance to the Loop Current was an important variable retained in the model, and enoploteuthid density in 2017 was similar to density in 2015 despite the lack of a strong northern penetration of the 2017 Loop Current, the factor plot for year is obscure.

The onychoteuthid paralarval density final GAM had an AIC of 242.0 with 20.3% DE (Table 3). Variables retained in the model, with

associated Δ AIC, were factor year (8.5), salinity (7.7), water depth (4.5) and SSH (4.1). Similar to the overall squid model, response plots from the onychoteuthid GAM showed an increase in density where salinity ranged from 25 to 35 psu. While the onychoteuthid model also retained SSH, it differed from the overall squid and enoploteuthid models by revealing an increase in density of onychoteuthid paralarvae density with increasing SSH (>0.4 m; Fig. 6). Similar to the ommastrephid model, the onychoteuthid model also retained water depth, but again with differing results as onychoteuthid paralarval density increases with increasing water column depth (>2000 m; Fig. 6). Onychoteuthid paralarval density was highest in 2017.

Table 3

Temporal and environmental variables retained in the final generalized additive models for all squid paralarvae combined and for the most abundant families. Change in Akaike Information Criterion (AIC), change in deviance explained (DE) and estimated P-values validate the importance of individual variables in the model.

Model	Parameter	Δ AIC	Δ DE
All Squid Final AIC: 880.0 Final DE: 29.1%	Julian Day***	46.4	16.7%
	Salinity**	11.5	4.9%
	Sea Surface Height **	8.5	3.9%
Ommastrephidae Final AIC: 388.2 Final DE: 17.2%	Time*	6.2	3.2%
	Water Depth***	17.5	11.3%
	Distance to Loop Current***	13.4	8.5%
Enoploteuthidae Final AIC: 327.9 Final DE: 16.6%	Distance to Loop Current***	10.3	5.9%
	Sea Surface Height	5.6	4.6%
	Year (2016*)	2.3	2.2%
Onychoteuthidae Final AIC: 242.0 Final DE: 20.3%	Year (2016**, 2017*)	8.5	10.7%
	Salinity*	7.7	8.7%
	Water Depth*	4.5	4.7%
	Sea Surface Height	4.1	5.7%

*P < 0.05, **P < 0.01, ***P < 0.001.

4. Discussion

Squid paralarvae were broadly distributed over the sampling area, implying that the northern Gulf is a well-mixed system and may be an important spawning area. During the three-year study, squid paralarvae were present in over 76% of the stations sampled with mean densities per survey ranging from 3.5 to 17.1 paralarvae 1000 m⁻³. Due to varying sampling methods, comparing abundance to other studies is difficult; however, observed densities of this study are similar to values reported for surveys conducted in the north Atlantic Ocean (Diekmann and

Piatkowski, 2004) and tropical Pacific Ocean (Boehlert et al., 1992). To date, 23 offshore families of squid are known to reside in the northern Gulf (Judkins, 2009; Judkins et al., 2017). During this study, 12 of those 23 families were identified, with Ommastrephidae being the dominant family collected followed by Enoploteuthidae and Onychoteuthidae, respectively. Other surveys conducted in the Gulf and north Atlantic Ocean observed these families (as paralarvae, juveniles, and adults) as the dominant families collected or within the top ten most abundant families (Diekmann and Piatkowski, 2004; Vecchione and Pohle, 2002; Judkins et al., 2017; Judkins and Vecchione, 2020.) These families have been observed as prey for large predatory fishes (swordfish, tunas, sharks) for the north Atlantic Ocean (Logan et al., 2013; Staudinger et al., 2013) and potential prey items for sperm whales in the northern Gulf (Judkins et al., 2013), with ommastrephids being the dominant cephalopod collected. Thus, it is not surprising that ommastrephid, enoploteuthid, and onychoteuthid paralarvae comprised the dominant taxa observed in these surveys, representing an essential component of the pelagic food web in the northern Gulf.

Temperature and salinity have been observed as important variables in habitat suitability models for early life stages of cephalopods (Zaragoza et al., 2015). Julian day (which highly correlated to SST) was the dominant factor influencing squid paralarval abundance, which increased from spring through summer, indicating a preference for summer hatching. While some squids can spawn throughout the year, warmer conditions are known to improve growth of paralarvae and to enhance reproductive success of adults (Dawe et al., 2000; Boyle and Rodhouse, 2005). During spawning season, some species of squids will move closer to shore to spawn to ensure paralarvae will hatch in areas with periods of optimal productivity (Gasalla et al., 2010). The northern Gulf is heavily influenced by freshwater flow from the Mississippi River, which delivers abundant nutrients, resulting in increased primary production offshore (Lohrenz et al., 1997). Due to hydrodynamic

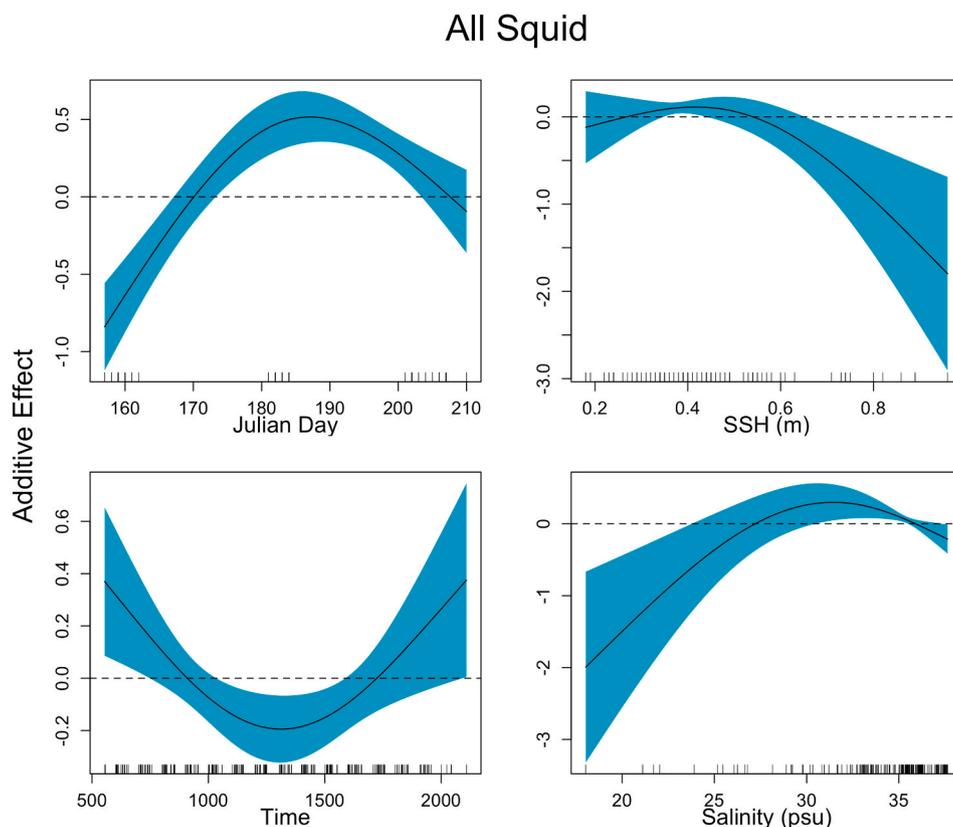


Fig. 3. Smoothed response plots of environmental variables that influence all squid paralarvae density during the 2015–2017 surveys based on the final generalized additive model (GAM). A dashed line is displayed on each plot at y = 0. Tick marks along the x-axis denotes observed values of the variable and shaded areas represent 95% confidence intervals (Sea surface height = SSH).

Ommastrephidae

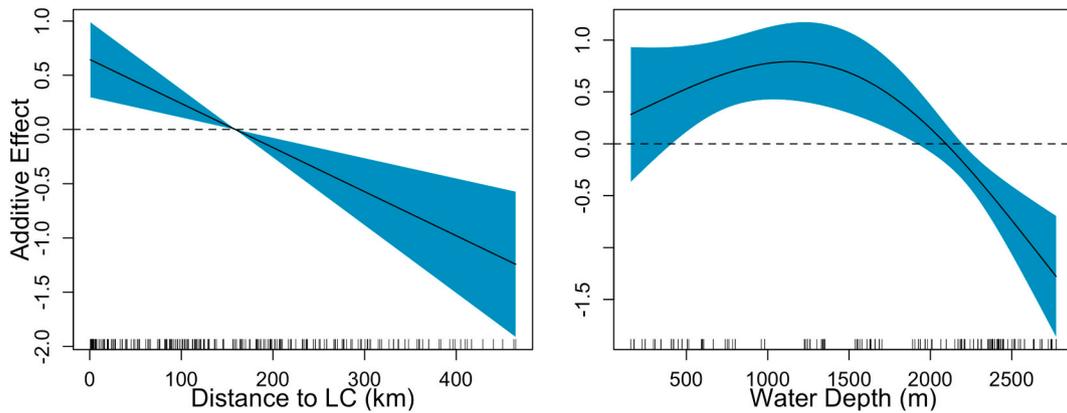


Fig. 4. Smoothed response plots of environmental variables that influence ommastrephid paralarvae density during the 2015–2017 surveys based on the final generalized additive model (GAM). A dashed line is displayed on each plot at $y = 0$. Tick marks along the x-axis denotes observed values of the variable and shaded areas represent 95% confidence intervals (Loop Current = LC).

Enoploteuthidae

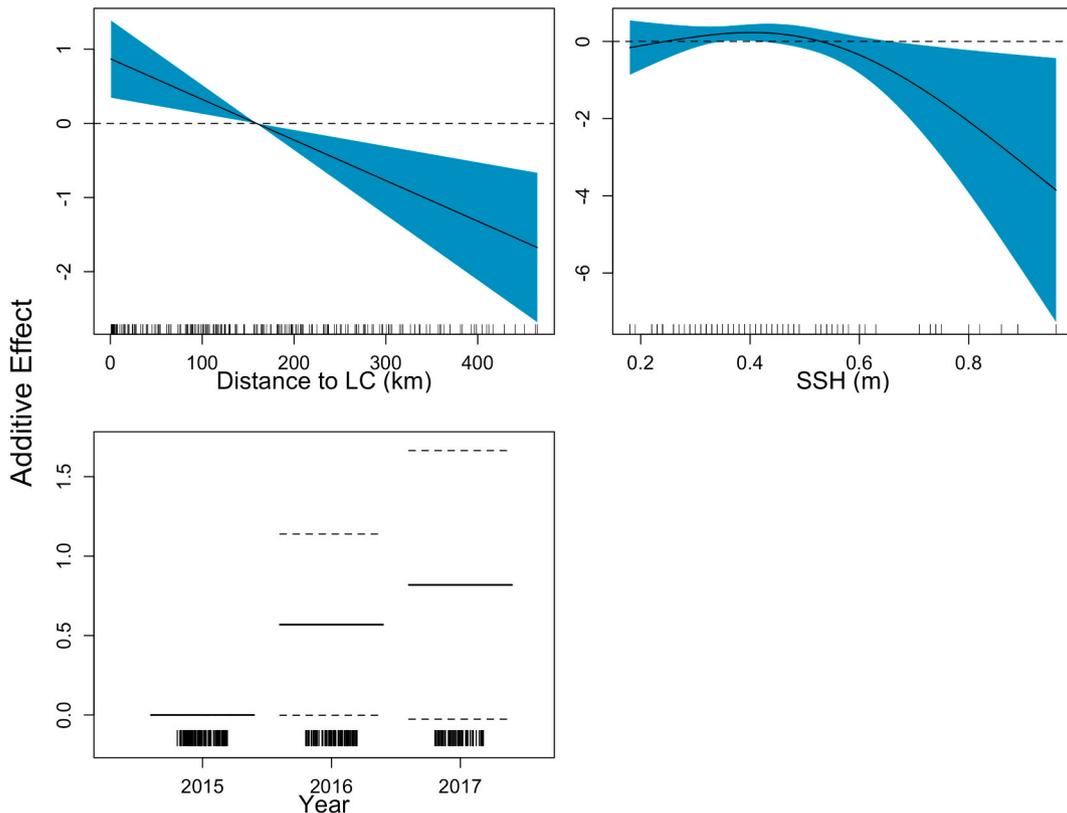


Fig. 5. Smoothed response plots of environmental variables that influence enoploteuthid paralarvae density during the 2015–2017 surveys based on the final generalized additive model (GAM). A dashed line is displayed on each plot at $y = 0$. Tick marks along the x-axis denotes observed values of the variable and shaded areas represent 95% confidence intervals (Loop Current = LC; Sea surface height = SSH). Dotted lines on the factor year plot represent standard error bars.

convergence between riverine and oceanic waters, nutrients accumulate creating desirable habitat for fish larvae as food sources increase (Grimes and Finucane, 1991). While ocean salinity averages 35 psu, higher abundances of squid paralarvae were at lower salinities ranging from 28 to 35 psu. These values are well above the lower reaches of salinity tolerance for cephalopods (17–20 psu; Judkins, 2009; Oesterwind and Schaber, 2020), which may indicate that waters influenced by

the Mississippi River discharge serve as desirable paralarval habitats, with elevated primary productivity enhancing the early-life survival and recruitment of squids. Some ommastrephids are known to migrate from oceanic waters to areas on the continental shelf during certain seasons (Clarke, 1996), and Erickson et al. (2017) found that ommastrephid paralarvae off the Atlantic coast of Florida peaked from April–July. Ommastrephid paralarvae densities in this study were higher at lower

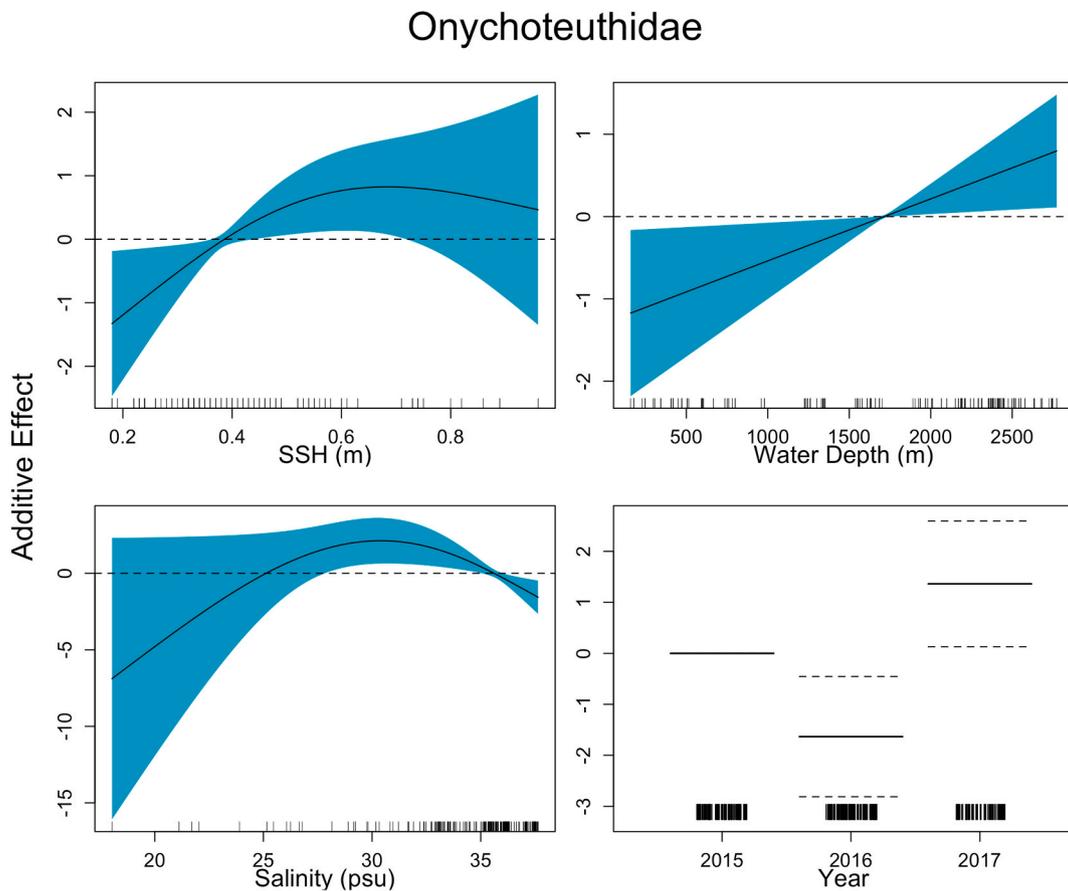


Fig. 6. Smoothed response plots of environmental variables that influence onychoteuthid paralarvae density during the 2015–2017 surveys based on the final generalized additive model (GAM). A dashed line is displayed on each plot at $y = 0$. Tick marks along the x-axis denotes observed values of the variable and shaded areas represent 95% confidence intervals (Sea surface height = SSH). Dotted lines on the factor year plot represent standard error bars.

water depths suggesting a preference for outer shelf and slope stations exposed to coastal water.

The distribution of squid paralarvae in this study coincides with areas highly productive for pelagic fish larvae, including billfishes, swordfish, tunas and dolphinfishes (Rooker et al., 2012, 2013; Kitchens and Rooker, 2014; Cornic et al., 2018). Each of these taxa was found in greater densities in close proximity to the Loop Current and fronts or areas of confluence associated with eddies, which are known to promote primary and secondary production (Davis et al., 2002). Distance to the Loop Current was retained in the ommastrephid and enoploteuthid model, showing an increase in density of ommastrephid and enoploteuthid paralarvae as distance to the Loop Current decreased, with densities peaking near the margin of the current. While distance to the Loop Current was not retained in other models, the associated eddies may influence the distribution of squid paralarvae. Squid abundance was higher overall in areas with low SSH, which is characteristic of frontal boundaries or possibly near cyclonic (cold core) eddies in the Gulf. Primary productivity is often elevated along frontal boundaries or in water masses associated with cold core eddies due to upwelling of cold, nutrient-rich waters from depth, creating desirable nursery habitats for pelagic larvae (Bakun, 2006). Distribution and abundance of squid paralarvae is known to coincide with upwelling areas that enhance the retention of paralarvae, as well as their food resources, leading to higher survival rates (Rodhouse et al., 2014). Conversely, onychoteuthid paralarvae densities increased with greater SSH and greater water depths implying that stable water of the open-ocean stations provided more suitable habitat for this family. Onychoteuthid species in the Mediterranean Sea were also observed avoiding mixed waters formed by mesoscale events (Zaragoza et al., 2015).

Time of day was a significant variable in the overall squid model indicating a diel vertical migration pattern. Several species of pelagic squid, including the two most abundant families collected in this study (Ommastrephidae and Enoploteuthidae), generally reside in the meso-pelagic zone at later ontogenetic stages but migrate into the epipelagic zone at night to feed (Roper and Young, 1975; Judkins, 2009; Judkins and Vecchione, 2020). The presence of these deep-water families in our daytime collections was not surprising because pelagic paralarvae of cephalopods, as with fishes and other invertebrates, often spend the first few weeks or months of life in the surface waters before moving to habitats occupied later in life (Roper and Young, 1975; Leis, 2010). It's possible time of day was not retained in the ommastrephid and enoploteuthid models because paralarval ML averaged less than three mm and ontogenetic vertical migration shifts may not have occurred. Judkins and Vecchione (2020) observed that smaller individuals (<15 mm ML) of both Ommastrephidae and Enoploteuthid were found throughout the water column. Onychoteuthid juveniles do not exhibit vertical migration at the scale sampled by Judkins and Vecchione (2020), which agrees with time not being retained in that model. Many of the deep-water families of the Gulf were not collected in this survey of the upper 100 m of the water column. Some families of squid not collected in these surveys, such as Bathyteuthidae, do not utilize the epipelagic zone during the early life phase and reside below the depth (>600 m; Judkins and Vecchione, 2020) of the net tows of this study. Adding nighttime sampling and increasing the depth of the tows would enhance diversity (families) of squid paralarvae from this region surveyed in the northern Gulf. Diekmann and Piatkowski (2004) obtained 200% more specimens in night and twilight tows compared to daytime samples.

Findings from this study demonstrate that several families of squid

spawn in the northern Gulf and utilize the near surface waters of this area as paralarval habitat during the summer. This is potentially a mechanism to exploit the increased production along upwelling zones associated with mesoscale features, as well as increase in primary and secondary production linked to the Mississippi River discharge. However, utilizing this region may make them vulnerable to anthropogenic disturbances at the sea surface, including oil spills. Additionally, model results indicate that paralarvae of squid taxa in the northern Gulf are capable of diel vertical migration. Quantitative studies like this one that provide time series data are necessary to begin characterizing patterns that identify desirable paralarval developmental habitats and oceanographic conditions that support squid during early life.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2021.103572>.

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