Variability of Paralarval-Squid Occurrence in Meter-net Tows from East of Florida, USA

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Abstract - We attempted to determine cross-shelf, diel, and seasonal distribution patterns of paralarval cephalopods off eastern Florida during a 5-year study that employed both open-net and discrete-depth closing-net sampling. Based on our 303 samples, abundant and common squid taxa included the squid *Doryteuthis* spp., which tended to be in coastal and intermediate waters, and *Abralia* cf *veranyi* (Eye-Flash Squid), *Illex* spp. (shortfin squid), and Ommastrephidae Type A (which could include *Ommastrephes bartramii* [Neon Flying Squid] and *Ornithoteuthis antillarum* [Atlantic Bird Squid]), mostly in intermediate and Florida Current waters. Species diversity and abundance were usually greatest in Florida Current waters versus coastal and intermediate waters. Overall, however, few patterns were obvious from these samples. Accessory sampling to examine variability indicated that a large number of samples are required to infer detailed distribution patterns. We also found that the difference in variation between sampling at a fixed location and sampling within a moving parcel of water was not consistent.

Introduction

Little is known about the ecology of paralarval cephalopods in some areas, in spite of the importance of cephalopods in marine ecosystems and fisheries. Knowledge about the distribution and species abundance of paralarval squids within different water masses can help provide insight into the influence of factors such as current systems on squid ecology (Dawe and Beck 1985, Gonzalez et al. 2005, Vidal et al. 2010) and spawning sites (Bower 1996). Occurrence of paralarval squids can also provide information on relative abundance of species and may be useful as an indicator of general ecology (Jorgensen 2007, Vecchione 1987).

The early life-history of cephalopods has often been studied by sampling with standard zooplankton gear, similar to studies of ichthyoplankton. We sampled paralarval cephalopods over a 5-y period using a small boat and plankton nets from the Smithsonian Marine Station (SMS), Fort Pierce, FL. This study was initially planned as a continuation of earlier opportunistic studies of the systematics and ecology of paralarval cephalopods (e.g., Vecchione et al. 2001). Our goal was to determine species composition and relative abundance along a standardized transect across the continental shelf into the Florida Current/Gulf Stream system (hereafter, Florida Current), including vertical distribution. However, as sampling

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progressed, we noted that high sampling-variability raised questions about whether each tow was representative of species composition and relative abundance for a given time and location. Therefore, we conducted 4 additional series of tows to examine scales of temporal and spatial variability of paralarval occurrence in these zooplankton tows.

Paralarval octopods collected in this study were reported by Roper et al. (2015). Adams (1997) reported taxonomic observations and some general distribution patterns of the squid paralarvae collected in this study. Here, we summarize the occurrence of paralarval squids east of central Florida, with emphasis on sampling variability and the need for a large number of samples to infer with confidence occurrence patterns for paralarval squids.

Field-Site Description

We conducted all sampling along a transect extending offshore from Fort Pierce Inlet, FL. This is an area where bottom depth increases rapidly and the Florida Current is particularly close to shore. Fixed-station locations and designations are illustrated in Figure 1. We established 13 sampling stations at 3.7-km (2 nautical miles) intervals eastward from 3.7 km off the coast across the continental shelf to a maximum distance of 48.1 km offshore. This transect was designed to span 3 water masses—coastal, intermediate, and Florida Current. The identity of each water mass was determined by the temperature and salinity data collected concurrently with sampling (Adams 1997).

Methods

We conducted 12 sampling trips, each a series of daily excursions from SMS, with a 12-m boat at opportunistic times of year between February 1987 and August 1991 (Table 1). We collected all specimens aboard the R/V *Sunburst* using 333-µm mesh plankton nets on 1-m–diameter ring frames, towed with 3-point bridles from a wire with a hydrodynamic depressor weight. Sampling duration was 15 minutes and we recorded flow-meter readings at the beginning and end of each tow. An internally recording conductivity–temperature–depth (CTD) instrument was attached to the towing wire between the net and the depressor to record temperature, conductivity (to calculate salinity), and pressure (depth) at 15-sec intervals continuously throughout the tow. Prior to each 15-min tow, the CTD was placed ~0.5 m below sea surface for at least 5 min to equilibrate before it was lowered to the desired sampling depth.

We collected most samples during daytime hours, but collected discrete-depth samples taken in 1990 during both day and night. Following each tow, we thoroughly rinsed the net with seawater, retained the contents, and fixed them in a solution of 4% formaldehyde in buffered seawater for at least 1 week before rinsing in fresh water, removing and sorting paralarvae, and preserving them in 50% isopropanol. We calculated the displacement volume of total zooplankton for each sample as a rough estimate of plankton biomass. At the end of each sampling day, we downloaded CTD data to a computer at SMS. We recorded sampling-station latitude and longitude for all stations using Loran during early trips, or GPS when it became available on the boat.

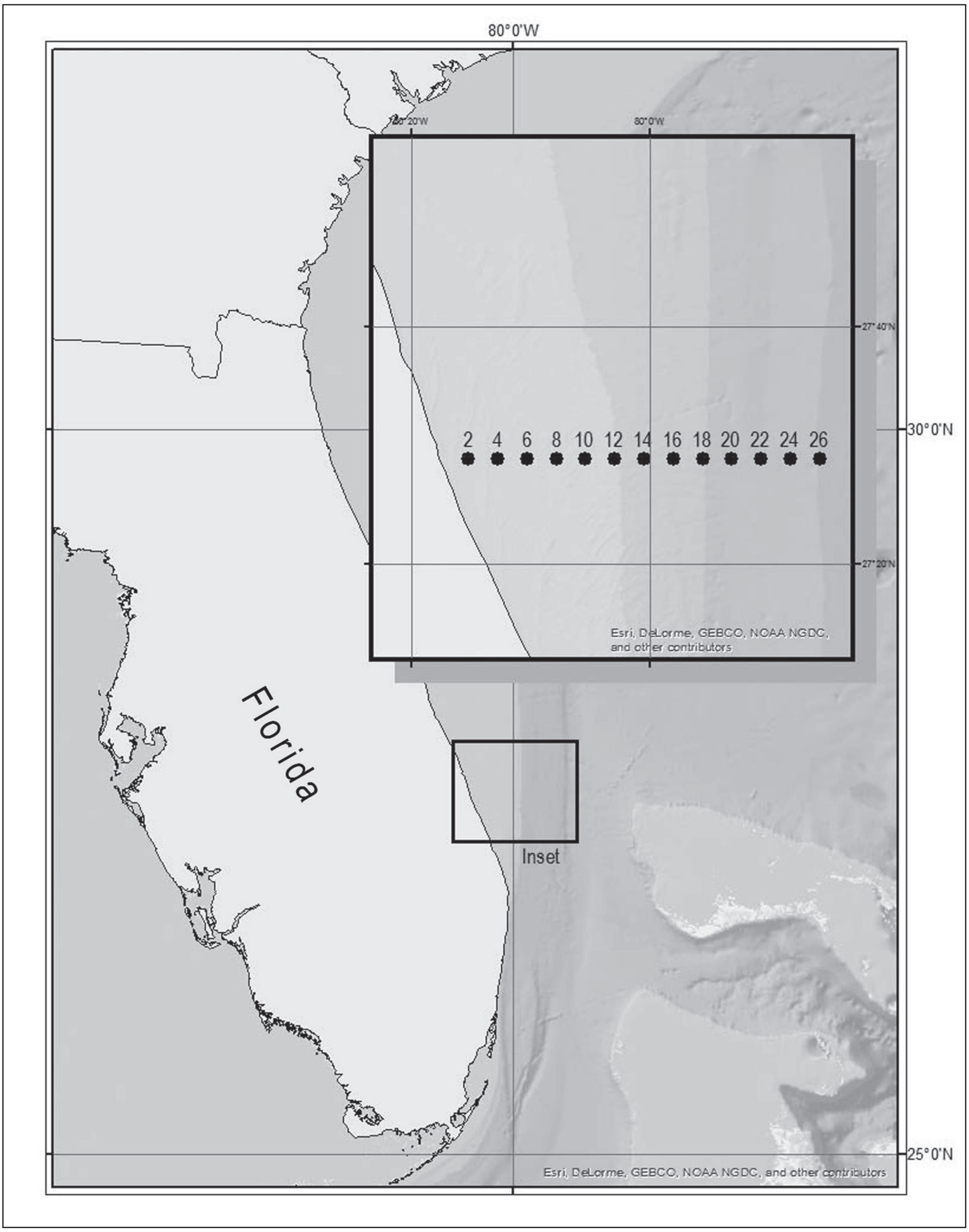

Figure 1. Transect-sampling stations for cross-shelf distribution patterns and species abundance of squid paralarvae during the study period (1987–1991). Numbers in inset box are the station designations based on the distance offshore (in nautical miles [nmi]; 2 nmi = 3.7 km) of Fort Pierce Inlet.

We employed the following 5 sampling protocols

(1) We conducted standard transect sampling across the continental shelf off of Fort Pierce Inlet over a 2-day period for each trip (except the first; Table 1) throughout this 5-y study (1987–1991). Each daily transect was comprised of 9 stations, located ~3.7 km apart. We collected paralarval samples with a double-oblique, open-net tow for 15 mins from the surface to ~200 m, or as near bottom as possible at station depths <200 m. Net depth was determined in all protocols based on wire angle and the amount of wire deployed. To examine daily variability during the 2 days of transect sampling, we sampled the 3.7–33.3-km stations on 1 day and the 48.1–18.5-km stations the other day, providing overlap along the mid-transect area 18.5–33.3-km offshore. We did not undertake transect sampling during February, May, October, or November of any year.

(2) To determine the vertical distribution patterns, we conducted separate discrete-depth sampling throughout the 5-y study. During 1 trip-day, we made 3 "quasi-replicate" tows for each of 3 target depths with closing nets. We selected at random the order in which depths were sampled. The 3 depths were near-surface (~3-m depth so the net would be below the boat wake), mid-depth (half the depth of the bottom tow, up to 100 m, depending on the station depth), and near-bottom (200-m maximum, but variable depending on the bottom depth of a station). The near-surface net was simply fished open for 15 min. We rolled nets for mid-depth and near-bottom with the flow meter inside, attached to a messenger-operated, double-trip mechanism, lowered to a target depth, opened, towed horizontally for 15 min, and then closed.

(3) In 1990, we assessed diel variability with both day and night sampling. At the 37.0-km station, we collected replicate closing-net samples at depths of 10 m, 60 m, and 120 m during the day and at night, yielding a total of 18 samples: 9 day samples

Table 1. Summary of sampling trips (multi-day sampling events). Protocol 1: Transect sampling; Protocol 2: Daytime discrete-depth sampling; Protocol 3: Nighttime discrete-depth sampling; Protocol 4: Repetitive sampling at a fixed station 37.0 km offshore; Protocol 5: Repetitive sampling while following a drogue buoy starting at the station 37.0 km offshore. Note that no transect sampling occurred during February, May, October, or November in any year. Asterisk (*) = not replicated.

		Protocol				
Trip	Date	1	2	3	4	5
1	25 February 1987				x*	
2	9–11 June 1987			x		
3	27–29 July 1987			x	x	
4	21–23 September 1987		x	x*		
5	11–13 January 1988			x		
6	11–14 April 1988			x	x*	
7	30 August–2 September 1988	x				
8	5–8 December 1988			x	x	
9	27 March 1989			x		
10	31 July–2 August 1989		x	x		
11	17–26 July 1990	x	x	x	x	x
12	6–15 August 1991	x	x		x	x

(3 for each depth), and 9 night samples (3 for each depth). Unfortunately, we had to pool the samples by depth due to variation from designed sampling because of changing weather conditions.

(4) We conducted repetitive sampling on 3 consecutive days at a fixed location in 1990 and 1991 to determine short-term and daily variability at a mid-transect station assumed typical of the transect. We planned 15-min, double-oblique, open-net tows at the single location 37.0 km offshore, yielding a total of 9 samples per day and a total of 27 samples for the 3 days. In 1991, on the third day, the boat experienced mechanical issues so we changed the nine 15-min tows to three 30-min tows; thus, we collected only 21 samples for the oblique series in 1991.

(5) To examine small-scale variability within a discrete parcel of water, we conducted sampling for a single day in 1990 and in 1991, by following a surface-water parcel tracked by a drogue buoy for comparison with the 37.0-km fixed geographic location described above in Protocol #4. We marked a water mass with a window-shade drogue buoy, beginning at 37.0 km offshore. We made 9 double-oblique open-net tows at the location of the drogue-buoy as it drifted with the current, yielding a total of 9 samples for each year.

Results

Overall patterns

Hydrographic observations are presented in Adams (1997). Our sampling extended from coastal water, through the transitional waters, and into the Florida Current. In general, the Florida Current tended to occur in the area from 33.3 km to 48.1 km offshore. Coastal water occurred from 3.7 km to ~14.8 km offshore, but this area varied due to the continuous changes in the position of the Florida Current system. Transitional waters consisted of a narrow band between the coastal waters and the Florida Current waters. Typically, cooler waters are located towards the coast and the warmer waters are offshore in the Florida Current, but thermal stratification by depth was almost always evident.

Due to limitations of using a small boat far offshore in variable weather conditions and at night, and occasional problems with sampling gear, the actual numbers of samples collected often did not match the planned numbers described above in Methods. We collected a total of 303 samples.

Of 1450 cephalopods collected, we identified a total of 1303 paralarval squids belonging to 25 taxa (Table 2). Table 2 also presents the total numbers for taxa collected from the standard transect series from 1987 to 1991. Although the numbers of squid paralarvae per tow varied from 0 to 58, many tows caught 0 (Table 3), especially inshore. When tallied by taxon, numbers were generally 0–3 per tow. Tows generally filtered ~1000 m^3 of water, but this volume varied greatly. Except for the most abundant taxa, standardizing the catch for such low numbers to relative abundance as n/1000 m^3 only added variability.

In the strandard transect sampling, we collected >100 specimens for 4 taxa, and 3 other taxa were represented by >50 specimens. The inshore squid *Doryteuthis* spp. was most abundant in coastal waters from 1989 to 1991, and in intermediate waters during 1987 and 1988. We consistently detected *Abralia* cf. *veranyi* (Rüppell) (Eye-Flash Squid) throughout the study area, but it was most abundant in the intermediate and Florida Current waters during 1987 and 1988 and mostly in the Florida Current in 1989 and 1991. Ommastrephidae Type A (*Ommastrephes bartramii* (Lesueur) [Red Flying Squid], possibly mixed with *Ornithoteuthis antillarum* Adam [Atlantic Bird Squid]) was most abundant in the Florida Current for all 5 years, but was also found in the coastal and intermediate waters. We caught *Illex* spp. (shortfin squid) primarily during 1988; it was dominant in the Florida Current waters, but was also found in the intermediate water region.

Transect sampling (Protocols 1, 4, and 5)

Of the transect samples, only 76% contained squids; positive samples were as low as 50% on 1 trip (Table 4). Negative samples tended to be those collected

Table 2. Number (*n*) of paralarval squid specimens collected, ranked by *n* in regular transect samples. Total includes all protocols, transect refers to collections during standard-transect sampling (Protocol 1).

Taxon	Total number collected (*n*)	Number collected during transect sampling (*n*)
Abralia cf. *veranyi* (Rüppell)	599	226
Illex spp.	250	134
Doryteuthis spp.	160	129
Ommastrephidae Type A	215	111
Pyroteuthis margaritifera (Rüppell)	157	76
Ommastrephidae Type B	203	65
Pterygioteuthis spp.	146	53
Enoploteuthis anapsis Roper	33	10
Selenoteuthis scintillans Voss	21	10
Leachia atlantica (Degner)	13	8
Enoploteuthis leptura (Leach)	11	4
Octopoteuthis sp.	10	5
Abraliopsis sp. A	17	5
Onychoteuthis cf. *banksi* (Leach)	22	4
Abraliopsis sp. B	15	3
Unidentified Histioteuthidae	5	2
Thysanotethis rhombus Troschel	2	2
Onychoteuthis sp.	2	2
Walvisteuthis jeremiahi Vecchione et al.	5	2
Cranchia scabra Leach	2	2
Ancistrocheirus lesueuri (d'Orbigny)	3	1
Liocranchia sp.	1	1
Unidentified Pyroteuthidae	88	0
Unidentified Ommastrephidae	10	0
Unidentified Enoploteuthidae	9	0
Unidentified Lycoteuthidae	4	0
Unidentified Cranchiidae	3	0
Liguriella sp.	3	0
Brachioteuthis sp.	1	0
Helicocranchia sp.	1	0

at the inshore stations. Only 1 trip had no negative stations; therefore, the minimum number of squid specimens per station was generally 0. Maximum number of specimens per station varied from 4 to 58, with no clear seasonal pattern, but we often collected higher numbers offshore. The maximum number of taxa per station ranged from 3 to 11, and the range of maximum specimens per taxon was 2–22, with no clear patterns. Other than when numbers were very low, we found no clear relationship between numbers of specimens and numbers of taxa per

Table 3. Number (*n*) of samples collected per year using 5 different Protocols, including (1) oblique sampling of standard transect, (2 and 3) discrete-depth sampling, including diel comparisons, (4) repetitive sampling at a fixed location 37.0 km offshore, and (5) sampling in the vicinity of a drogue buoy launched 37.0 km offshore. N/A = (not applicable); protocol was not conducted that year. Trips = multi-day sampling events.

	1987	1988	1989	1990	1991	Total	% of Total *n* with squids
Number of trips	4	4	2	1	1	12	
Protocol 1: Transect sampling							
n	53	61	27	6	9	156	
n with squids	46	42	18	4	9	119	76%
Protocols 2 and 3: Discrete-depth sampling							
n	15	21	9	18	18	81	
n with squids	9	14	4	12	14	53	65%
Protocol 4: Fixed-location (37.0-km station) sampling							
n	N/A	N/A	N/A	27	21	48	
n with squids	N/A	N/A	N/A	25	21	46	96%
Protocol 5: Drogue-buoy (beginning at the 37.0-km station) sampling							
n	N/A	N/A	N/A	9	9	18	
n with squids	N/A	N/A	N/A	9	9	18	100%
Grand total							
n	68	82	36	60	57	303	
n with squids	55	56	22	50	53	236	78%

Table 4. Dates of transect sampling (Protocol 1) trips, with summary of samples and squid paralarval specimens (spec) and taxa collected. *n* - number of transect stations (sta).

Sampling trip	*n*	*n* with squids	Max spec/sta.	Max taxa/sta	Max spec/taxon
June 1987	18	15	15	7	6
July 1987	17	16	22	5	20
September 1987	18	15	7	4	2
January 1988	17	14	27	8	11
April 1988	14	7	58	11	22
August–September 1988	16	10	6	3	4
December 1988	14	11	48	8	22
March 1989	9	8	19	10	6
July–August 1989	18	10	12	6	7
July 1990	6	4	4	3	2
August 1991	9	9	35	9	15

station (i.e., larger numbers of specimens did not necessarily equate to greater taxonomic richness).

When we detected the high apparent variability in these non-replicated transect samples, we began accessory sampling (Table 5) to determine how representative a 15-min tow would be for either a fixed location (Protocol 4) or, alternatively, within a moving parcel of water (Protocol 5). The number of tows required to collect all of the taxa found in 9 samples at a fixed location on a particular day was 6–9. Returning to the same station on consecutive days added a little, but not substantially, to the documented diversity of the station. Sampling in a drifting parcel of water required fewer tows (3–6) to document the total diversity found in the series. Except for 1 outlier (6 taxa), the diversity in each full-day series, whether at the fixed location or drifting, was fairly consistent (10–14 taxa per day). The number of squid specimens per tow and specimens per taxon, however, varied greatly among tows within a day, and both among days in a year and between years.

Short-term variability in inferred abundance of even the most common and abundant species was also high (Figs. 2, 3). This result was partly caused by variability in the amount of water filtered by a tow. The coefficient of variability (CV = ratio of standard deviation to mean) for catch of Eye-Flash Squid was 1.04–1.24 for fixed stations and 0.87 in July 1990. In August 1991 these coefficients were lower—0.5–0.57 for fixed stations and 0.80 in the drogue series.

When we pooled standard transect catches of abundant taxa for all years, we detected seasonal patterns, but none were very clear. Figure 4 shows the relative seasonal abundance of the 4 most common and abundant paralarval squid taxa. *Doryteuthis* spp. were most abundant in the summer months; however, we also collected specimens in the cooler months. Eye-Flash Squid was present year-round and

Table 5. Sets of 9 consecutive samples. Tows req = the number of consecutive 15-min tows that were required to collect all taxa found in the entire 9-tow series for that day. Added = the number of taxa added by sampling more than 1 day in the 3-day series for a fixed location. *On 9 August 1991, we were unable to follow the standard protocol of nine 15-min tows and collected only 3 samples from longer tows. N/A = not applicable.

Date	Number of taxa	Tows req	Specimens/tow	Taxa/tow	Added
1990 Fixed location (37.0-km station, Station 20 on Fig. 1)					
23 July 1990	14	9	1–8	1–5	N/A
24 July 1990	6	6	0–5	0–3	0
25 July 1990	10	9	0–7	0–6	1
1990 Drogue-buoy series (beginning at the 37.0-km station)					
20 July 1990	12	3	3–10	2–7	N/A
1991 Fixed location (37.0-km station)					
7 August 1991	11	8	9–28	3–8	N/A
8 August 1991	11	7	6–29	4–8	2
9 August 1991*	10	3*	27–35	6–9	0
1991 Drogue-buoy series (beginning at the 37.0-km station)					
12 Aug 1991	12	6	10–57	5–8	N/A

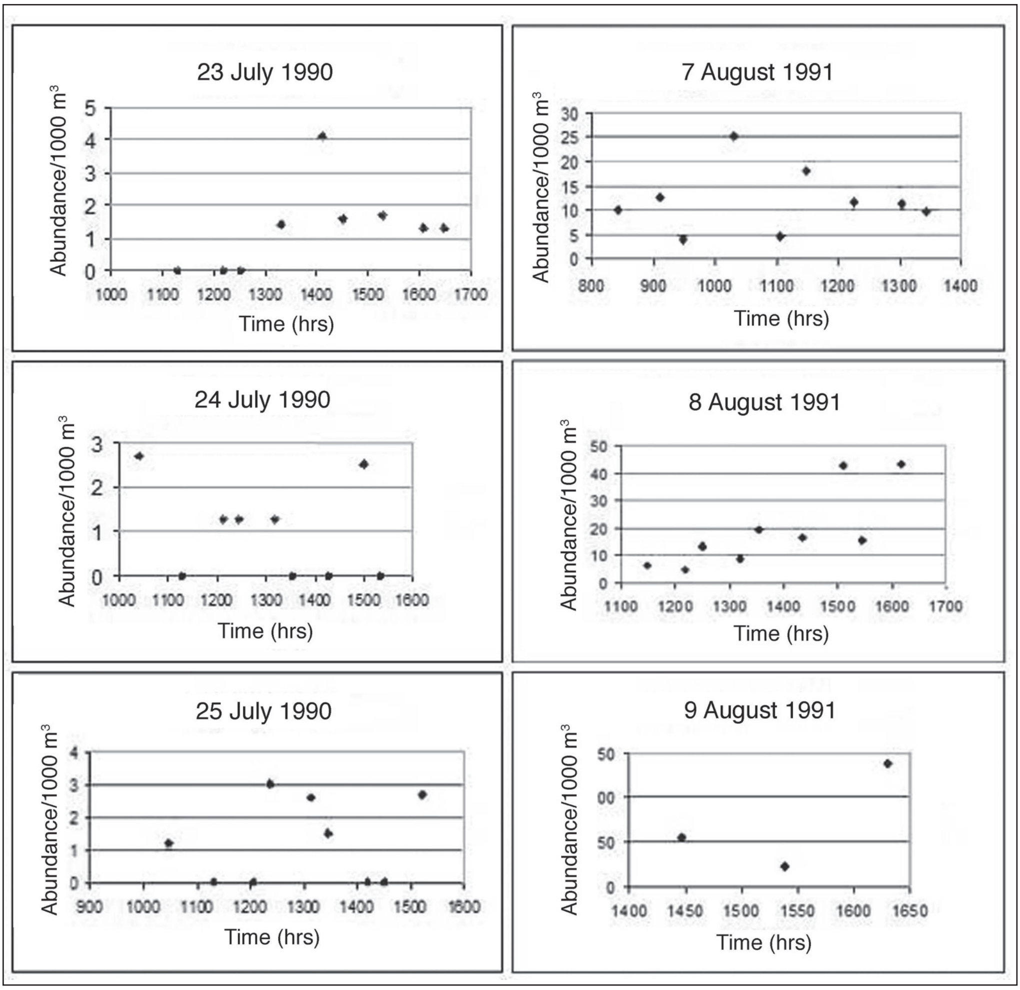

Figure 2. Abundance of paralarval *Abralia* cf *veranyi* in consecutive tows (Protocol 4) at the 37.0-km_station on 3 consecutive days in 1990 and 1991.

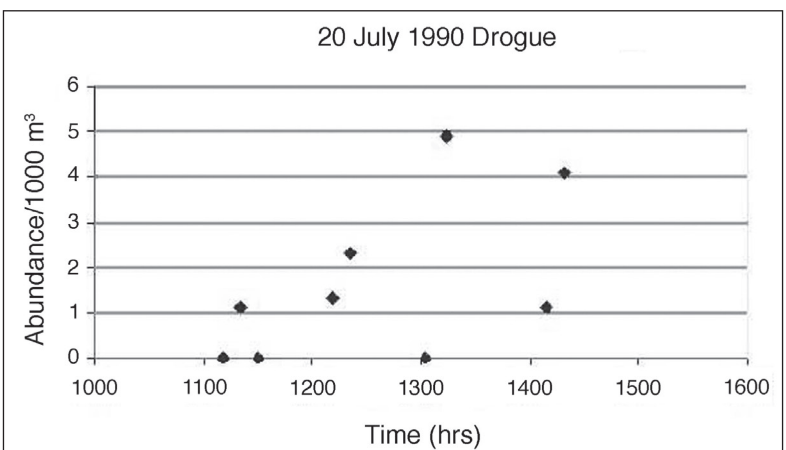

Figure 3. Abundance of paralarval *Abralia* cf *veranyi* in consecutive tows while following a drogue buoy (Protocol 5), starting at the 37.0-km_ station in 1990.

dominant in August. We collected few Eye-Flash Squid in September, but larger numbers occurred in December and January. Ommastrephidae Type A (Red Flying Squid and Atlantic Bird Squid) were the most abundant in April, June, and July, but not very prevalent in the other months. We observed Shortfin Squid primarily in winter, but they were present throughout the year except during late summer.

Depth distribution (Protocol 2) and diel variability (Protocol 3)

Discrete-depth sampling (Protocol 2) included 4 sets of triplicate samples and 1 set of 5 replicates, plus 1 set of triplicate day/night comparisons (Protocol 3). These samples included 0–19 squid paralarvae. Occurrence of taxa in individual samples was quite variable. In general, we collected more specimens and taxa at mid-depth than near-surface or near-bottom. *Pterygioteuthis* sp. was consistently abundant in all mid-depth samples during the diel comparison, both day and night. Otherwise, variability was so great (Table 6) that we could make no consistent inferences about vertical distribution or diel migration for any taxon.

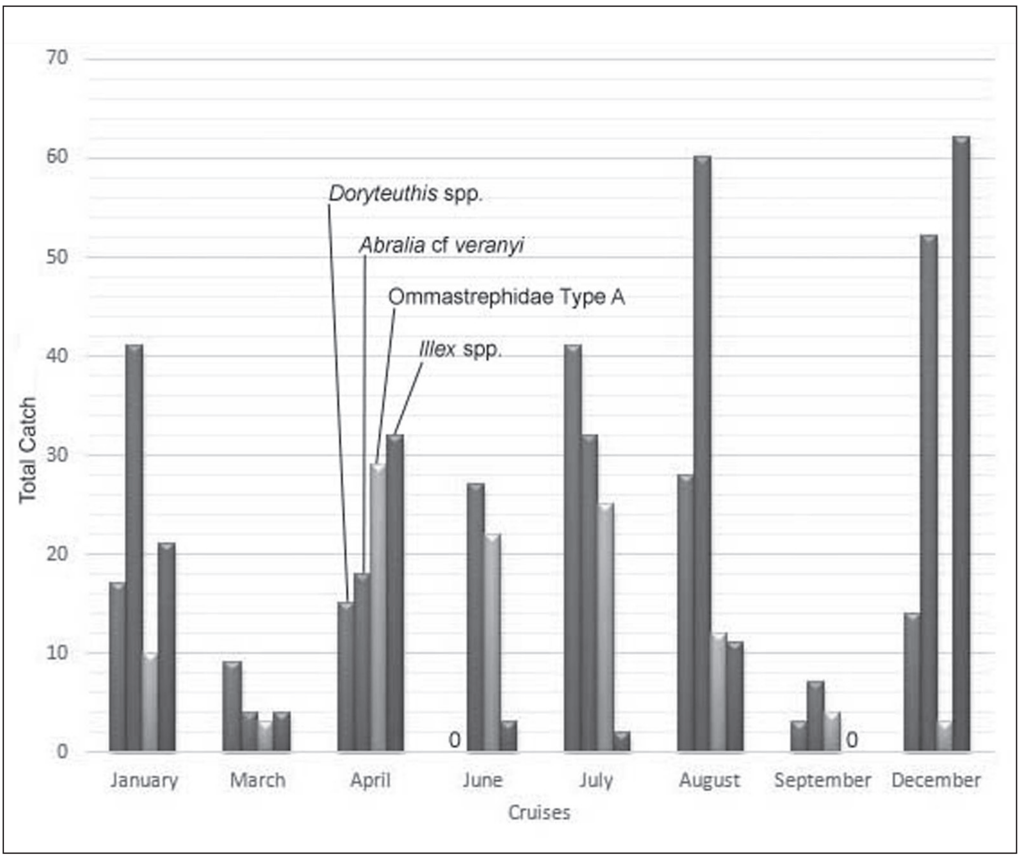

Figure 4. The relative dominance of the 4 most common and abundant paralarval squid taxa observed during transect sampling (Protocol 1) in pooled samples from different seasons offshore of Fort Pierce Inlet during the present study. No transect sampling occurred during February, May, October, or November of any year.

Discussion

The overall characteristic of all of the analyses of these data was overwhelming variability. Based on the accessory sampling, it appears that a full day at each station, using standard meter nets, would be required to effectively assess the diversity and abundance of squid paralarvae in the study area. However, our addition of 2 sampling days (Days 2–3 in Protocol 4) did not contribute substantially to inferences of diversity or abundance. Of course, if the goal is to infer fairly small-scale spatial patterns, as it was here, spending a day at each station would not only necessitate greatly increased time at sea, but would also cause spatial patterns to be confused with potential day-to-day variability over the 13 days (at least) that would be required. For discrete-depth sampling, triplicate sampling was generally not sufficient to infer meaningful patterns.

The difference in variation between sampling at a fixed location and sampling within a moving parcel of water was not consistent between the years. It appeared that fewer samples may be required with Protocol 5 (drogue buoy) than Protocol 4 (fixed station) to document the full paralarval diversity present on a given day. The low coefficients of variability (~1 or less) in both the fixed-location and drogue sampling indicate that the mean abundance inferred from these 9 samples would be a reasonable estimate at that station and date, at least for the most abundant species. Although we have only 2 such comparisons, there may be little advantage in the more difficult sampling plan of trying to stay within a discrete water mass, compared to focusing on a geographic location; however, this would probably not be true in an area where there is great temporal variability in the water masses present at a location (e.g., where river plumes or current eddies likely occur).

Our inability to identify all specimens confidently to species also impaired the strength of inferences that we could determine from the data. For example,

Table 6. Discrete-depth sampling. Replicates = number of samples per depth; Taxa = number of taxa collected in the entire series; >3 spec = number of occurrences when any taxon had >3 specimens in a single sample; taxon = the taxon that had >3 specimens in a sample; where = depth stratum and number of samples in which taxon with >3 specimens was found; surf = near-surface; mid = mid-depth; bot = near-bottom; D = daytime samples; N = nighttime samples.

Sampling trip	Replicates	Taxa	>3 species	Taxon	Where
Feb 1987	1	2	0		
Jul 1987	3	5	1	Ommastrephidae type B	1 surf
Sep 1987	1	1	0		
Apr 1988	3	6	2	*Doryteuthis* sp.	1 mid, 1 bot
Sep 1988	1	3	0		
Dec 1988	3	10	1	*Illex* sp.	1 mid
Aug 1989	3	6	0		
Jul 1990 (D)	3	4	3	*Pterygioteuthis* sp.	3 mid
Jul 1990 (N)	3	10	3	*Pterygioteuthis* sp.	3 mid
14 Aug 1991	1	4	2	*A. veranyi*	1 surf
				Ommastephidae type A	1 surf
15 Aug 1991	5	8	5	*A. veranyi*	2 mid, 2 bot
				Pterygioteuthis margaritifera	1 bot

the seasonal pattern for the inshore squid *Doryteuthis* (see Fig. 2) may have been confused by the presence of both *D. pealeii* Lesueur (Longfin Inshore Squid) and *D. plei* Blainville (Slender Inshore Squid) in the catches. Similarly, *Illex* spp. may have comprised as many as 3 species which we could not distinguish morphologically. Although we think that most of the *Abralia* that we caught were Eye-Flash Squid, some *A. redfieldi* Voss (Redfield's Enope Squid) may have been mixed in, particularly among the smallest specimens.

We collected >300 samples; thus, we are able to describe some very general patterns for the squid paralarval fauna of the study area. The highest species abundances and diversity of paralarval squids consistently occurred in the Florida Current waters. Roper et al. (2015) reported that the highest total abundance of the paralarval octopods caught in the same collections was also found offshore in the Florida Current. The Florida Current is part of the Gulf Stream western boundary current that flows from the Straits of Florida to beyond the Grand Banks (Rowell and Trites 1985). The Gulf Stream System generally flows offshore of the 200-m isobath (~37.0–48.1 km off the east coast of Florida, but farther offshore to the north). Edge filiments and warm-core and cold-core eddies are characteristic of the Gulf Stream system and the first 2 can transport entrained animals onto the continental shelf (Vecchione 1981).

The total squid abundance was greatest between the 33.3-km and 40.7-km stations in 1987, between the 37.0-km and 48.1-km stations in 1988, and between the 44.4-km and 48.1-km stations in 1989, and then moved back to the 33.3-km and 40.7 km stations in 1990 and 1991. These results suggest that squid distribution across the continental shelf varies as the Florida Current moves on- and offshore.

The discrete-depth series showed that highest total abundance and diversity of paralarval squids was within the mid-depth zone. Similarly, the highest total abundance of paralarval squids from the 1990 diel comparison was at the mid-depths both day and night. Roper et al. (2015) also found that the greatest abundance of octopod paralarvae in the same collections as examined in this study occurred at mid-depth.

Limited sampling can contribute valuable information about paralarval biology, taxonomy, and the developmental morphology of the species collected (e.g., Gonzalez et al. 2010, Shea 2005). However, sampling for distribution requires coverage that is more comprehensive. Paralarval surveys have been proposed to be effective for assessment of cephalopod populations (Jorgensen 2007, Vecchione 1987) and determination of spawning grounds (Bower 1996, Goto 2002). The present study was constrained by the capabilities of the available boat and its small winch. The gear used here, a 1-m diameter ring net with a towing bridle, has been widely used for zooplankton studies (UNESCO 1974) but is not an optimum method for collecting cephalopod paralarvae. Many studies of paralarval distribution and abundance have been byproducts of ichthyoplankton surveys (e.g., Jorgensen 2007). These studies often use a combination of oblique tows with "bongo" frames (paired nets rigged so that there is no bridle in front of the net mouths) and surface tows with some form of neuston nets (e.g., CalCoFI [Koslow and Allen 2011], MARMAP program [Vecchione et al. 2001]). Surface samples sometimes catch extraordinary numbers of squid paralarvae (Vecchione 1999), but the surface fauna in our study area was not sampled by the present methods. Vertical distribution and diel migration is generally better assessed using a multiple-net opening/closing gear, such as a MOCNESS (Goldman and McGowan 1991) or rectangular midwater trawl 1 + 8 (Shea and Vecchione 2010) but their use is not possible from a small boat.

The current study has provided information on various scales of temporal and spatial variability, but few clear patterns were obvious. Our recommendations to researchers considering similar studies are: (1) use a vessel with sufficient capability for conducting operations in squalls and at night; (2) choose an effective sampling gear, with a mouth opening larger than a 1-m diameter and without a towing bridle in front of the net mouth; and (3) compile a large number of samples (suggested minimum of several hundred) in order to make confident inferences about distribution.

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