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Associations between lobster phyllosoma and gelatinous zooplankton in relation to oceanographic properties in the northern Gulf of Mexico

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Abstract

Lobster phyllosoma are known to associate with large cnidarian medusae; however, direct quantitative observations are difficult because gelatinous zooplankton are extremely fragile, and the phyllosoma easily detach from their host when sampled by plankton nets. We provide the first large scale quantitative information of the distribution of this association using an in situ imaging system, with synoptic measurements of water column properties. All phyllosoma were identified as slipper lobsters (*Scyllarus chacei*) and were associated with previously unreported "hosts" such as small hydromedusae, doliolids, and siphonophores in the northern Gulf of Mexico. Along the shelf, phyllosoma were more likely to be present at greater depths and higher salinities. Approximately 30% of the 347 lobster phyllosoma imaged were attached to at least one gelatinous organism, and salinity and depth were positively related to the probability of attachment on 30 October, but did not show a significant relationship for the other days of sampling. Many of the phyllosoma were larger than the gelatinous organisms to which they were attached, and some gelatinous zooplankton showed damage likely from feeding by the phyllosoma. In this coastal environment, gelatinous zooplankton tended to be more abundant in the same offshore region where phyllosoma occurred, so these gelatinous "hosts" may provide a steady food supply in the more oligotrophic waters on the outer shelf. Similar complex interactions among zooplankton may influence the life histories of other species, hindering our ability to forecast ecosystem level processes until the population level consequences of species interactions are fully understood.

KEYWORDS
behavior, ecological interactions, oceanography, plankton imaging, scyllaridae, species associations

1 | INTRODUCTION

Gelatinous zooplankton (referred to here as "jellies") are an ecologically diverse group of organisms that includes pelagic cnidarians, ctenophores, and pelagic tunicates. Jellies are abundant and have a large impact on trophic interactions and carbon cycling (Greer et al., 2013;

Sweetman, Smith, Dale, & Jones, 2014); however, their life histories and interactions with other organisms remain poorly described, partially due to the destructive nature of traditional plankton net sampling (Hamner et al., 1975; Remsen, Hopkins, & Samson, 2004). Although jellies are unpalatable for many zooplanktivores (Bullard & Hay, 2002), they have a suite of specialized or opportunistic

predators, such as sea turtles and several fish species (Arai, 2005; D'Ambra, Graham, Carmichael, & Hernandez, 2015; Mianzan, Pájaro, Alvarez Colombo, & Madirolas, 2001), and can serve as alternative pathways for carbon cycling in marine food webs (Robinson et al., 2014). Some gelatinous zooplankton contain portions of their bodies that are high in carbon content and could be preferentially eaten by predators (Milisenda et al., 2014; Shenker, 1985).

In addition to their roles as predators and prey in the planktonic ecosystem, jellies are involved in other types of ecological interactions within the marine zooplankton, including parasitism (Brandon & Cutress, 1985; Chiaverano, Graham, & Costello, 2015; Phillips, Burke, & Keener, 1969; Towanda & Thuesen, 2006), commensalism (Browne & Kingsford, 2005; Condon & Norman, 1999; Phillips, Burke, & Keener, 1969), and mutualisms (Gasca & Haddock, 2004; Hay et al., 2004; Towanda & Thuesen, 2006). Describing complex behavioral relationships within zooplankton communities, especially as they relate to the distributions in the context of oceanographic properties and survival of organisms, is necessary to understand marine ecosystem functioning (McManus & Woodson, 2012; Menden-Deuer & Kiørboe, 2016; Visser, 2007).

Some planktonic crustacean and larval fish taxa are known to associate with gelatinous zooplankton for both shelter and food (Laval, 1980; Lynam & Brierley, 2007; Phillips, Burke, & Keener, 1969). Lobster phyllosoma of the family Scyllaridae ("slipper lobsters") have been shown to associate with some types of medusae, but the adaptive advantage of this association is likely multifaceted (Browne & Kingsford, 2005; Herrnkind, Halusky, & Kanciruk, 1976). It has been hypothesized that phyllosoma attaching to gelatinous zooplankton may serve as a method for the larvae to utilize water movements that allow them to remain closer to shore (Booth, Webber, Sekiguchi, & Coutures, 2005; Sekiguchi, Booth, & Webber, 2007). However, recent evidence from molecular diet studies and aquaculture supports the idea that phyllosoma often rely on gelatinous zooplankton as prey (O'Rorke et al., 2015; Suzuki, Murakami, Takeyama, & Chow, 2006; Wakabayashi, Nagai, & Tanaka, 2016). This has been substantiated by captive observations of Palinurid and Scyllarid phyllosoma feeding on gelatinous zooplankton (Saunders et al., 2012; Wakabayashi, Sato, Hirai, & Tanaka, 2012), with additional evidence provided by mouth and gut morphologies that appear suited to feed on soft, fleshy foods, such as gelatinous zooplankton and detritus (Mikami, Greenwood, & Takashima, 1994), as well as other adaptations to resist stinging nematocysts (Kamio, Wakabayashi, Nagai, & Tanaka, 2016; Kamio et al., 2015; Wakabayashi, Nagai, & Tanaka, 2016). Most phyllosoma are widely thought to be generalist predators (Connell, O'Rorke, Jeffs, & Lavery, 2014; Jeffs, Nichols, Phleger, & Mooney, 2004; Saunders et al., 2012) and attach to medusae in a non-selective manner (Wakabayashi, Sato, Hirai, & Tanaka, 2012). The two hypotheses of phyllosoma utilizing gelatinous zooplankton as transport assistants or food resources may not be mutually exclusive because there could be multiple benefits that maintain the phyllosoma-jelly association. Field observations of larval behavior have been difficult (Phillips & Sastry, 1980), or have been limited to phyllosoma attached to large, conspicuous

scyphomedusae (Phillips, Burke, & Keener, 1969). These complex relationships are likely important components of species life history and potentially useful for resolving recruitment processes, but the relationship between behaviors and oceanographic properties on fine spatiotemporal scales is not frequently examined.

Because the adult phase of benthic associated animals has a relatively small home range (often less than 1 km for lobsters; O'Malley & Walsh, 2013), larval dispersal is the dominant mechanism allowing these species to exploit new habitats (Booth et al., 2005; Chiswell & Booth, 2008; Cowen & Sponaugle, 2009), as well as sustain their populations through self-recruitment (Cowen, Paris, & Srinivasan, 2006; Cowen, Lwiza, Sponaugle, Paris, & Olson, 2000; O'Malley & Walsh, 2013; Sponaugle et al., 2002). These larvae, when present, tend occur over a large area, indicating that they have multiple spawning locations and can survive in a range of oceanographic conditions for weeks to several months (Butler, Paris, Goldstein, Matsuda, & Cowen, 2011; Jeffs, Nichols, Mooney, Phillips, & Phleger, 2004; McWilliam & Phillips, 2007; Phillips & McWilliam, 2009). The combination of long larval phase duration and resulting recruitment variability, together with slow adult growth with little horizontal movement, make lobsters extremely vulnerable to overexploitation (Hearn, 2006). Although currently unexploited in the Gulf of Mexico, some fisheries are currently shifting to Scyllarid lobster extraction due to the overexploitation of other crustaceans, namely the Palinurid ("spiny") lobsters (Duarte, Severino-Rodrigues, & Gasalla, 2010). This places a priority on understanding processes occurring in the phyllosoma larval stages of these animals, which include, but are not limited to, favorable transport to appropriate settlement grounds with adequate food supplies, while avoiding predators along the way. Although ecological interactions likely have minimal influence on larval dispersal, they can directly impact larval survival in several ways.

We provide the first high resolution, quantitative descriptions of phyllosoma abundances and associations with gelatinous zooplankton, along with sizes and identification of the jellies serving as hosts. In addition, using the variety of data obtained from in situ imaging, we explore ecological interactions between phyllosoma and gelatinous zooplankton in more detail, shedding light onto the oceanographic influences of this unusual relationship. These results may be applicable to our understanding of population connectivity and fisheries management for lobsters and other animals with similar pelagic life histories closely tied to abundances and distributions of other zooplankton taxa.

2 | MATERIALS AND METHODS

2.1 | In situ imaging

The In Situ Ichthyoplankton Imaging System (ISIIS: Cowen & Guigand, 2008) is used to quantify the abundances of phyllosoma and other mesozooplankton ranging in size from ~500 μm to 13 cm. ISIIS utilizes a shadowgraph optical technique, which projects a light source across an imaged water parcel, and the plankton that block the light

source are imaged as "shadows". When towed at a constant speed of ~2.5 m/s, the line scan camera (Piranha II Dalsa) shoots a continuous image with a scan rate of ~36,000 lines/s. Software breaks up the continuous image into individual frames with a 13 × 13 cm field of view and a ~45 cm depth of field. At a constant tow speed of 2.5 m/s, the ISIIS can sample 1 m^3 of water in ~7 s. The optical system is equipped with motor actuated wings for depth control operated by onboard software (GreenSea, Inc.), a Doppler velocity log (DVL, 600 micro, Navquest), and several sensors, including a CTD (SBE 49, Sea-Bird Electronics, Inc.), fluorometer (Eco FL RT, Wetlabs), photosynthetically active radiation (PAR) sensor (QCP2300), and dissolved oxygen (SBE 43, Sea-Bird Electronics, Inc.). Each of these sensors samples the marine environment at 6 Hz.

Imaging data came from four separate sampling days in the Fall of 2015 along three spatially separate meridional transects in the northern Gulf of Mexico, oriented from the north towards the south (Figure 1). These three sampling "corridors" were chosen to capture areas with different amounts of freshwater input as part of the CONsortium for COastal River-Dominated Ecosystems (CONCORDE). The Western corridor (WCORR) was closest to the Mississippi River outflow, with the Middle (MCORR) and Eastern (ECORR) corridors receiving progressively less influence from river discharge. For each day of sampling, ISIIS tows lasted 6 hr and were centered around noon local time, spanning a horizontal distance of ~54 km. The ISIIS was deployed in an undulating fashion, making a tow-yo pattern from ~1 m underneath the surface to ~4 m off the bottom, with an ascent/descent rate of ~30 cm/s for a range of bottom depths between 18 and 35 m.

2.2 | Net sampling

At the beginning and end of each ISIIS transect, net samples were taken to verify the organisms identified in the images and supplement the image data with biological samples for species level identification and measurement. Net samples commenced in the morning just after sunrise (~07.00 hr local time) at the inshore end of each corridor prior to the ISIIS deployment. A second series of net samples was taken in the afternoon (~14.00 hr local time) after retrieval of the ISIIS at the offshore end of each sampling corridor. Each net station consisted of a single Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS; Open Seas Instrumentation) tow with a 0.25 m^2 opening. The BIONESS was equipped with a CTD (SBE 19+, Sea-Bird Electronics, Inc.) and nine nets: six 333 μm nets and three 202 μm nets. The nets were fished in a tow-yo pattern to collect replicate samples within near-surface (0.5 m below surface), mid-, and near-bottom (2 m off the bottom) depth strata. Phyllosoma were sorted from the samples, identified, and imaged using a Canon Rebel T3i digital camera. Total length (distance from between the eyes to the base of the carapace) was measured to the nearest 0.001 mm for each net-captured phyllosoma using iSolution-Lite image analysis software.

2.3 | Data processing

Raw ISIIS images were processed using a series of steps implemented in ImageJ (version 1.49v, Rasband, 1997–2012). First, images underwent a flat-fielding procedure which removed image artifacts from the line scan camera (dark vertical lines) and evened out the background gray level. A customized segmentation program was then implemented on the flat-fielded images that extracted objects above a size threshold of 2000 pixels (minimum size of 3.4 mm equivalent spherical diameter) in area of the object, including holes in the center of an object with a black pixel border. These regions of interest (ROIs) were then classified manually using customized ImageJ "hotkeys" that allowed a user to classify organisms at a rate of ~2000/hr.
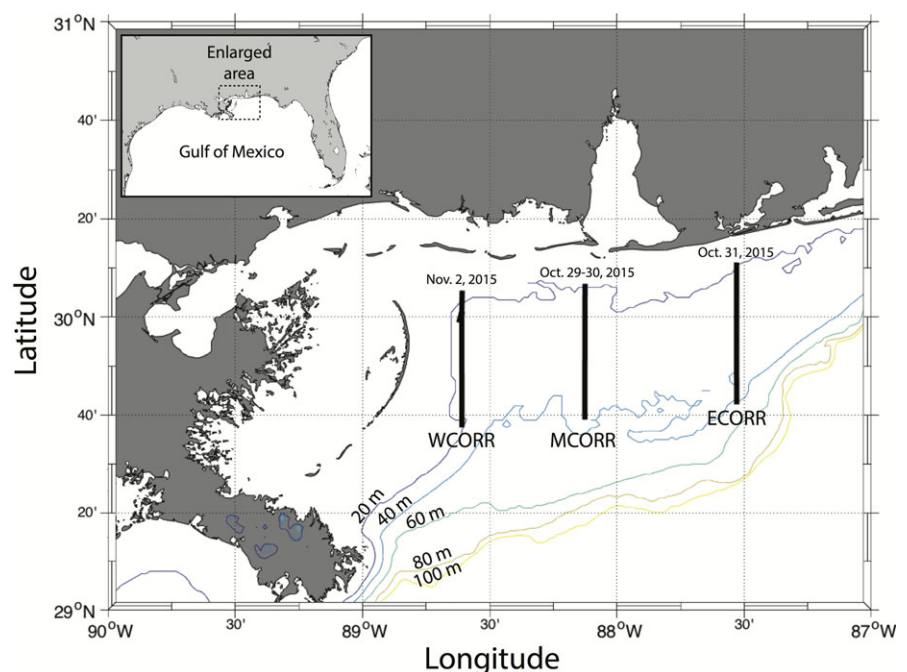

FIGURE 1 Map of the ISIIS sampling corridors in the northern Gulf of Mexico

For the MCORR transect on 30 October, 92,486 ROIs were classified into 13 different categories, including chaetognaths, hydromedusae, doliolids, larval fishes, shrimps, stomatopod larvae, ctenophores, marine snow, pteropods, siphonophores, and diatom chains, with two additional miscellaneous categories of "unknown" and "other." For the three other days of sampling, the regions of interest extracted from the segmentation program were scanned visually, and all phyllosoma larvae were saved without classifying other segments, which sped up the processing considerably. Imaged phyllosoma were manually measured in ImageJ from between the eyes to the posterior end of the carapace (appendages were not included in the size measurements) in the same manner as for the net samples. Each phyllosoma was measured in pixels, which was then converted to mm using the known field of view of the image (13 cm). We also determined that the phyllosoma was "attached" if one or more tips of the pereiopods intersected with a gelatinous zooplankter. Because the phyllosoma were measured in situ, some individuals were not completely visible within the field of view, but enough of the organism was imaged to positively identify it as a phyllosoma. If the tips of all of the appendages were not visible, then the phyllosoma was classified as "unknown" with regards to its attachment to a gelatinous zooplankter. For the gelatinous zooplankton attached to the phyllosoma, the organisms were identified to the lowest taxonomic level possible, and the length of the major axis (in the case of siphonophores and doliolids) or the bell diameter (in the case of hydromedusae) was measured and converted to mm.

Using the time stamp on the classified image file names, image data were merged with the environmental data using R (v.3.2.2, R Core Team 2015). The image and environmental timestamps were first converted to Julian time (percentage of a day). A custom R function identified the nearest time stamp from the environmental data, and the two datasets were then merged. To calculate abundances of different zooplankton taxa on 30 October, the count of each taxon was enumerated across a 1 m^3 bin (19.25 m of horizontal distance and 1–2 m vertical distance), and the environmental variables across that bin were averaged. This created a dataset of plankton abundances that was then merged to each individual phyllosoma to examine the background concentrations of different planktonic organisms in the phyllosoma's immediate vicinity. Distributions of abundant zooplankton taxa (chaetognaths, doliolids, and hydromedusae) on 30 October were interpolated among tow-yos using the R package akima (Akima & Gebhardt, 2015) and visualized using ggplot2 (Wickham, 2009).

2.4 | Statistical analyses

Logistic regression models were used in a descriptive fashion to understand the potential oceanographic influences on phyllosoma distribution and behavior (attachment to gelatinous zooplankton). Logistic regression models were fit using salinity and depth as predictor variables of phyllosoma presence and absence along the sampling transects within a given m^3 of sampled water (19.25 m horizontal distance). Each regression model was fit for a given day of sampling, and the significance of each explanatory variable (salinity or depth) was assessed using Wald tests. These models and all other statistical analyses were implemented in R using the logit link function, and each individual larva was assumed to be an independent sample, thus conforming to the expectations of parametric statistics. Correlations among predictor variables were assessed using the nonparametric Spearman rank correlation coefficients, which make no assumptions about the normality or variability in the data. The significance levels of these correlations were assessed using an approximation of the Student's t distribution in the 'Hmisc' package (Harrell et al., 2016). For tests of size differences between days, phyllosoma lengths were square root transformed to produce normal distributions (Shapiro-Wilk test for normality). Homoscedasticity of variance for phyllosoma lengths was confirmed using F tests. Analysis of Variance (ANOVA) was used on the transformed phyllosoma lengths to test for size differences between sampling corridors. For differences in depth, concentrations, and other variables between attached and unattached phyllosoma, Kruskal-Wallis tests were used because this test makes no distributional assumptions about the data.

3 | RESULTS

The water column was well mixed vertically, but there were horizontal gradients in a variety of physical properties of the water that differed among sampling corridors (Figure 2). The vertically mixed water column was influenced by the passage of Tropical Storm Patricia, which occurred less than 3 days before sampling began. Temperatures and salinities generally increased with decreasing latitude (and distance from shore), with the Spearman correlation between salinity and latitude of −0.7995 for all sampling days combined. There were, however, slight differences in these physical variables among the sampling corridors. WCORR had the lowest mean salinity (34.805), and the highest mean salinity was found on MCORR (35.194 and 35.199 on 29 and 30 October, respectively). ECORR had a mean salinity of 34.982, but the standard deviation of salinity along this transect was the lowest (0.1868) compared to the other transects. The within-transect temperature range was generally low (~1.5°C) with little vertical change among the transects.

The maximum transect average concentration of phyllosoma was 0.0656 ind./m^3, which occurred along the MCORR on 30 October. The lowest abundances were detected on WCORR, where only two individuals were captured at the most extreme southern end of the transect (average concentration of 0.000771 ind./m^3 for the entire WCORR – Figure 2). These two individuals were excluded from further analysis due to their rarity on this transect. Phyllosoma were essentially absent in the shallowest waters sampled north of ~29.95°N. A total of 33 phyllosoma collected in the plankton nets were identified to species level as *Scyllarus chacei*, and their concentrations collected from the nets were consistent with the average concentrations collected by the ISIIS in those offshore regions (Table 1). No phyllosoma were captured at the net tow stations at the northern heads of the transects.

FIGURE 2 Locations of lobster phyllosoma on 4 days of sampling in the northern Gulf of Mexico overlaying salinity measured with the ISIIS CTD. Each point corresponds to one individual phyllosoma, with the shape of the point indicating if the phyllosoma was attached to a gelatinous organism, was unattached, or could not be determined from the in situ image (unknown)
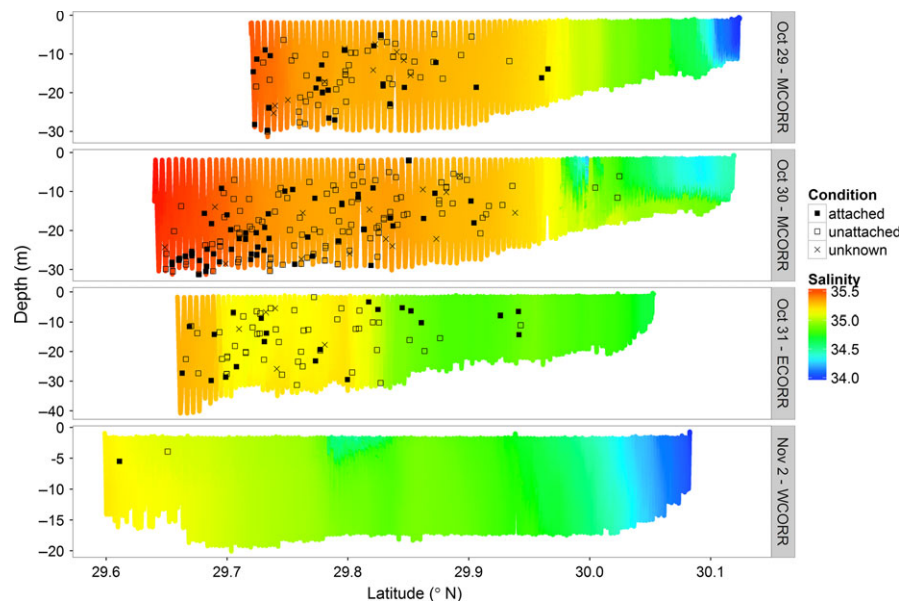
TABLE 1 Phyllosoma lengths and abundances collected with BIONESS plankton nets

Sample date	Sample station	Mean salinity (psu)	Depth bin (m)	Count	Total length range (mm)	Mean total length (mm)	Concentration (ind./m³)
10/30/2015	MCORR	35.65	1–39	9	3.12–10.96	6.07	0.151
10/30/2015	MCORR	35.65	1–39	2	2.96–4.04	3.50	0.010
10/30/2015	MCORR	35.65	1–39	4	4.42–6.23	5.20	0.039
10/31/2015	ECORR	35.35	1–40	3	6.40–9.52	7.61	0.027
10/31/2015	ECORR	35.34	27–40	3	5.39–6.12	5.80	0.035
10/31/2015	ECORR	35.34	14–27	2	4.90–7.15	6.02	0.029
10/31/2015	ECORR	35.29	1–40	2	2.91–3.67	3.29	0.045
10/31/2015	ECORR	35.28	27–14	1	6.43		0.008
10/31/2015	ECORR	35.27	1–14	6	3.98–10.82	7.01	0.044
11/2/2015	WCORR	35.30	6–13	1	8.01		0.017

Reported total lengths and densities of *Scyllarus chacei* observed in plankton net catches from the northern Gulf of Mexico during the Fall of 2015. ECORR, Eastern sampling corridor; MCORR, Mobile sampling corridor; WCORR, Western sampling corridor.

Phyllosoma were consistently oriented with a head-down posture (93.6% of individuals within 20° of facing directly downwards – examples in Figure 3). For some of the larger gelatinous zooplankton (e.g., *Liriope* spp.), the individuals with phyllosoma attached showed noticeable damage likely due to consumption by the phyllosoma (Figure 3g, h). Logistic regressions for each day of sampling demonstrated that phyllosoma were more likely to be present in a given m³ of sampled water when the sample was from deeper or saltier waters (Figure 4a, b). The exception to this trend was the ECORR (31 October), where phyllosoma presence/absence was not affected by the depth of sampling.

Of the 347 phyllosoma encountered in the ISIIS images, approximately 30% were attached to at least one gelatinous zooplankter, and this proportion was consistent among sampling corridors when sample size was adequate (Table 2). Although oceanographic conditions were significantly related to phyllosoma presence/absence on all sampling days, phyllosoma attachment probability was positively related to salinity and depth only on 30 October, which was also the day when phyllosoma were most abundant (MCORR – Figure 4c, d). Phyllosoma were most frequently attached to small hydromedusae, with siphonophores being the second most common association (mostly *Muggiaea* spp.). Phyllosoma were found to attach to doliolids only on the ECORR, which was where doliolids were most abundant compared to the other sampling corridors (data not shown). Sixteen individual phyllosoma were simultaneously attached to more than one gelatinous zooplankter, typically multiple hydromedusae, but in one instance, an individual was attached to a hydromedusa and a siphonophore (see Figure 3d, e). Examining the fine-scale background concentrations of different types of plankton on 30 October showed that phyllosoma attached to hydromedusae had significantly higher concentrations of large marine snow particles (>3.4 mm equivalent spherical diameter) in their immediate vicinity (Kruskal-Wallis, $p = .01779$) compared to unattached phyllosoma. The abundance of these large marine snow particles was also significantly
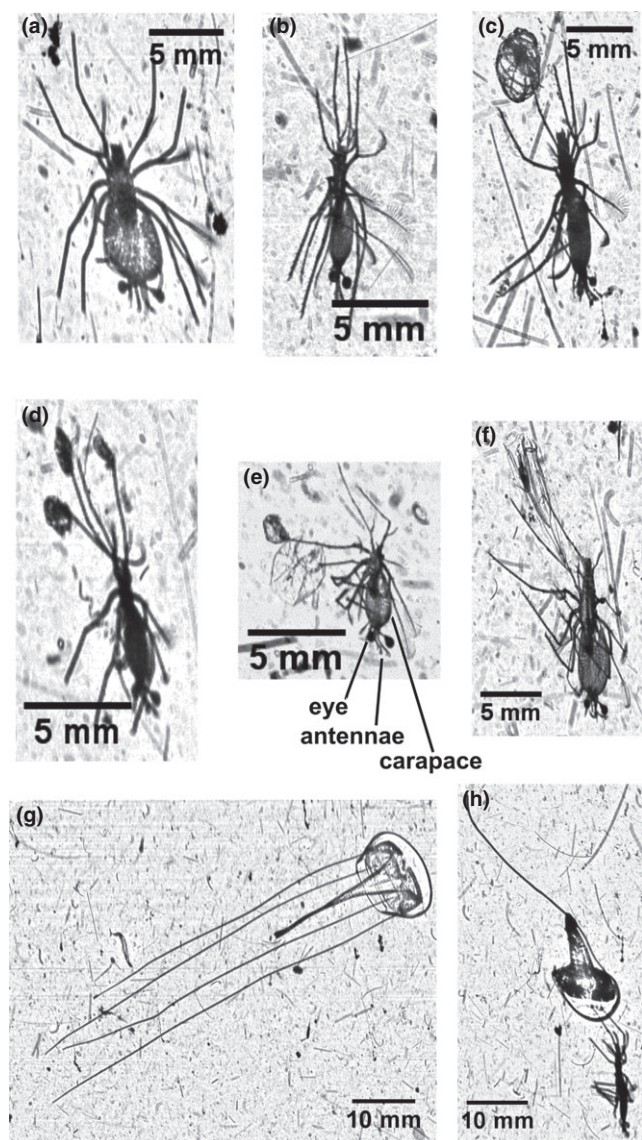
FIGURE 3 Example images of phyllosoma captured with the ISIIS. (a) and (b) phyllosoma larvae unattached to gelatinous zooplankton, (c) phyllosoma attached to a doliolid on the ECORR, (d) phyllosoma attached to three small hydromedusae, (e) phyllosoma attached to two hydromedusae, with phyllosoma parts labelled, (f) phyllosoma attached to *Muggiaea* spp. siphonophore, (g) individual *Liriope* spp. hydromedusa, and (h) same hydromedusa genus with phyllosoma attached (note that the *Liriope* spp. is missing three of the four tentacles and appears to be damaged). All images are shown with their natural in situ orientation

positively correlated with the abundances of hydromedusae and doliolids (Spearman rank correlation coefficient, 0.29 (p < .001) and 0.38 (p < .0001), respectively) throughout the transect on 30 October. The background concentration of particular jelly types was not significantly related to the type of attachment by the phyllosoma (e.g., hydromedusa vs. siphonophore – Figure 5), although background concentrations of all classified groups tended to be higher for phyllosoma attached to hydromedusae.

The sizes of lobster phyllosoma imaged were normally distributed, with no significant difference in size among sampling days

(Figure 6). Some smaller sizes appeared to be overrepresented on the ECORR (~6 mm in length); however, even the smaller sized phyllosoma tended to be larger than the average gelatinous "host" (Table 2). There was a significant increase in phyllosoma size with increasing salinity for larvae unattached to gelatinous zooplankton (p = .015, linear regression), but the fit was poor (R^2 = 0.0233). There was no significant relationship between salinity and size of attached larvae or any relationship between size and depth occupied by the phyllosoma. The smallest phyllosoma detected also tended to be associated with gelatinous zooplankton (Figure 6). On 30 October, these lower latitude areas further offshore and in deeper waters contained relatively high abundances of doliolids and hydromedusae (Figure 7). Chaetognaths, the most common mesozooplankton extracted with the segmentation algorithm, were more evenly vertically distributed throughout the water column but, similar the hydromedusae and doliolids, tended to be more abundant offshore.

4 | DISCUSSION

In situ imaging provided data previously unavailable with traditional sampling techniques, describing fine-scale distributions of lobster phyllosoma and providing a quantitative understanding of when and where they associate with gelatinous zooplankton. The deeper shelf waters were more likely to contain phyllosoma attached to gelatinous zooplankton, and these waters had higher abundances of gelatinous zooplankton, indicating that the phyllosoma may opportunistically attach to them. Considering potential benefits and costs for phyllosoma and gelatinous zooplankton related to this unique species interaction addresses several knowledge gaps that hinder our ability to describe population dynamics of species with complex life histories. These dynamics involve not only changing environmental conditions, but other species whose abundances (and their variability) are poorly described.

4.1 | Oceanographic conditions and behavior

Our results generally agreed with previous observations of abundant Scyllarid phyllosomas on the shelf (Booth, Webber, Sekiguchi, & Coutures, 2005; Sekiguchi, Booth, & Webber, 2007; Yeung & McGowan, 1991); however, in situ image data provided specific details on the factors potentially influencing these distributions. Examining the distribution of phyllosoma on a large scale revealed that individuals were almost exclusively found along the MCORR and ECORR transects, which had less freshwater influence compared to the WCORR. Along the transects (higher sampling resolution), there tended to be an increase in phyllosoma abundance further offshore (but still within shelf waters) and sometimes a higher probability of gelatinous zooplankton association. The fine-scale nature of the study, while providing unprecedented detail on the environment of phyllosoma and associations with gelatinous zooplankton, was necessarily limited in its spatial coverage. The positive relationship between phyllosoma presence and salinity may have not held if the sampling transects
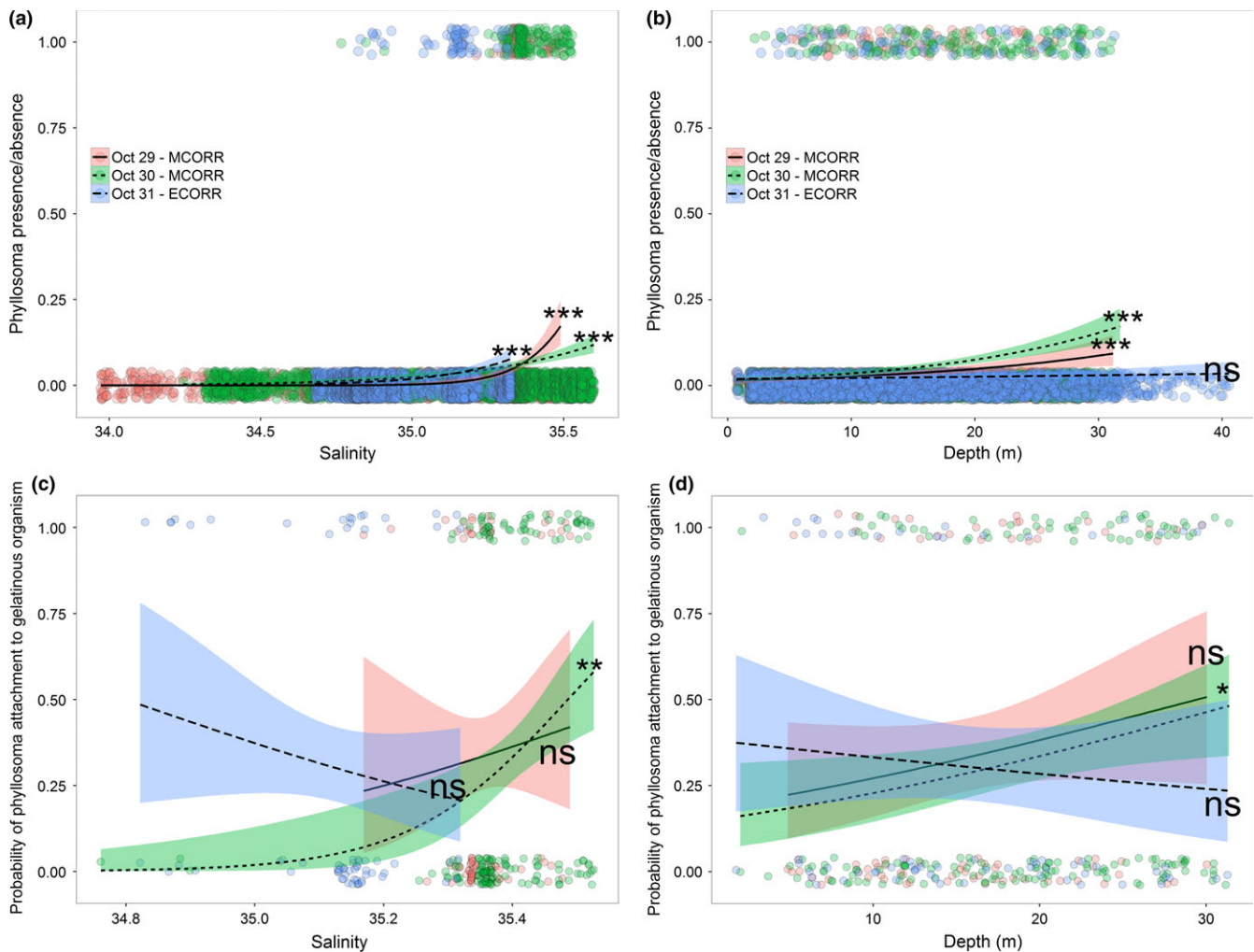
FIGURE 4 Phyllosoma presence (1) and absence (0) relative to measured (a) salinity and (b) depth along three of the four transects. Similar logistic regressions are fit to attached (1), and unattached (0) phyllosoma in relation to (c) salinity and (d) depth. The logistic regression (black line) is fit to the presence/absence or attached/unattached phyllosoma within a given m^3 of sampled water, and the shaded area corresponds to the 95% confidence interval of the logistic regression. Points indicating presence/absence and attached/unattached are given a random y-coordinate $\pm$ 0.05 to allow for improved visualization of the raw data. Symbols at the end of each logistic regression lines correspond to the significance levels from the Wald tests (ns, not significant; *$p < .05$, **$p < .01$, ***$p < .001$)

had continued to the shelf edge because Scyllarids are known to be the most abundant phyllosoma family nearshore (Sekiguchi, Booth, & Webber, 2007; Yeung & McGowan, 1991). Several zooplankton groups, including chaetognaths and gelatinous zooplankton, were more abundant at the offshore end of the transects, suggesting that phyllosoma inhabit similar environments to other mesozooplankton (Yeung & McGowan, 1991). In addition, there was a positive correlation with large marine snow aggregates, and the attached phyllosoma were found in areas with significantly higher abundances of marine snow. Convergent processes, known to produce marine snow aggregates and layers (Prairie et al., 2013; Stacey, McManus, & Steinbuck, 2007), may also correspond to locally high abundances of gelatinous zooplankton coming into contact with phyllosoma (Rothschild & Osborn, 1988), giving support to the idea that phyllosoma opportunistically attach to them. The impact of salinity changes on mesozooplankton abundance and community composition will be the subject of future research, shedding light onto some of the other

drivers of phyllosoma abundance that were not examined in this study.

Scyllarid lobster larvae are believed to make regular vertical migrations, with earlier stages occupying a shallower depth range (Phillips, 1981), which could lead to restricted larval dispersal (Yeung & McGowan, 1991). Our results did not show a relationship between size and depth (i.e., no evidence of ontogenetic vertical migration), consistent with observations of Minami, Inoue, & Sekiguchi (2001), although ontogenetic vertical migration has been documented for other phyllosoma species (Butler, Paris, Goldstein, Matsuda, & Cowen, 2011). If the phyllosoma were in the process of performing a diel vertical migration, they should have been at one depth extreme or the other of their migration when we sampled. Diel vertical migrations (Type I migration toward the surface at night, reviewed by Neilson & Perry, 1990) are known to occur in both Palinurid (Booth & Phillips, 1994; Rimmer & Phillips, 1979) and Scyllarid phyllosoma (Minami, Inoue, & Sekiguchi, 2001; Phillips,

TABLE 2 Statistics associated with phyllosoma attachments to gelatinous zooplankton. For the specific identifications of attached jellies (hydromedusae, siphonophores, and doliolids), the number found is given followed by the average size of the attached gelatinous zooplankter, with standard error in parentheses

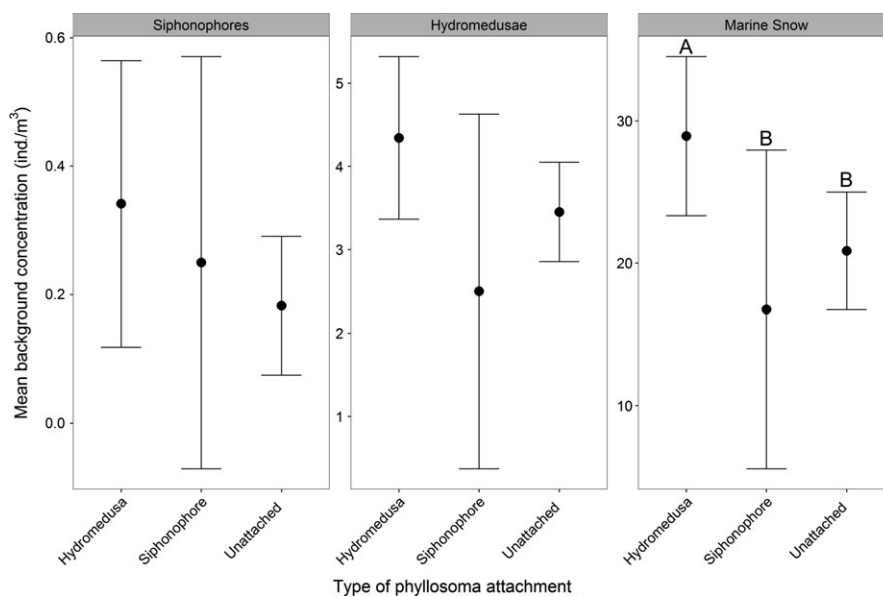| Date	October 29	October 30	October 31	November 2
Transect	MCORR	MCORR	ECORR	WCORR
Total Phyllosoma	86	184	75	2
Percent attached	30.23%	30.42%	28.00%	50.00%
Hydromedusae	20, 2.24 mm (0.17)	50, 3.01 mm (0.24)	15, 2.38 mm (0.32)	1, NA
Siphonophores	9, 5.91 mm (0.72)	12, 5.83 mm (0.84)	1, 7.50 mm	0
Doliolids	0, NA	0, NA	3, 4.30 mm (0.98)	0, NA
Unknown	3	2	7	0
Multiple jellies	5	8	3	0

FIGURE 5 Fine-scale (~20 m horizontal distance) background concentration of various groups of zooplankton and marine snow (±1.96 * standard error). Each panel corresponds to a different group background concentration (note the changing y axis scale). For the marine snow panel, a and b refer to significant differences assessed using Kruskal-Wallis tests
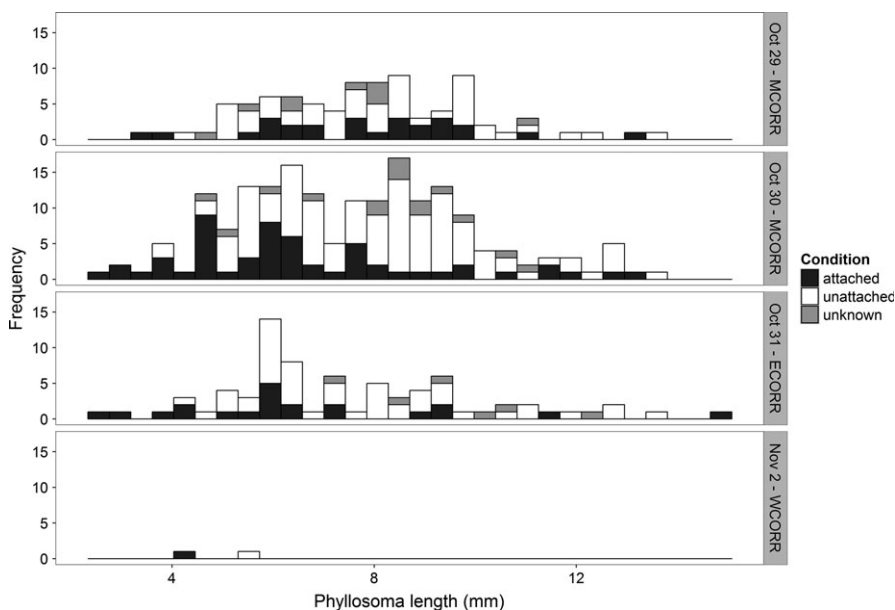

FIGURE 6 Histograms of phyllosoma lengths (mm). The fill of the bar indicates the number of individual phyllosoma attached or unattached to gelatinous zooplankton
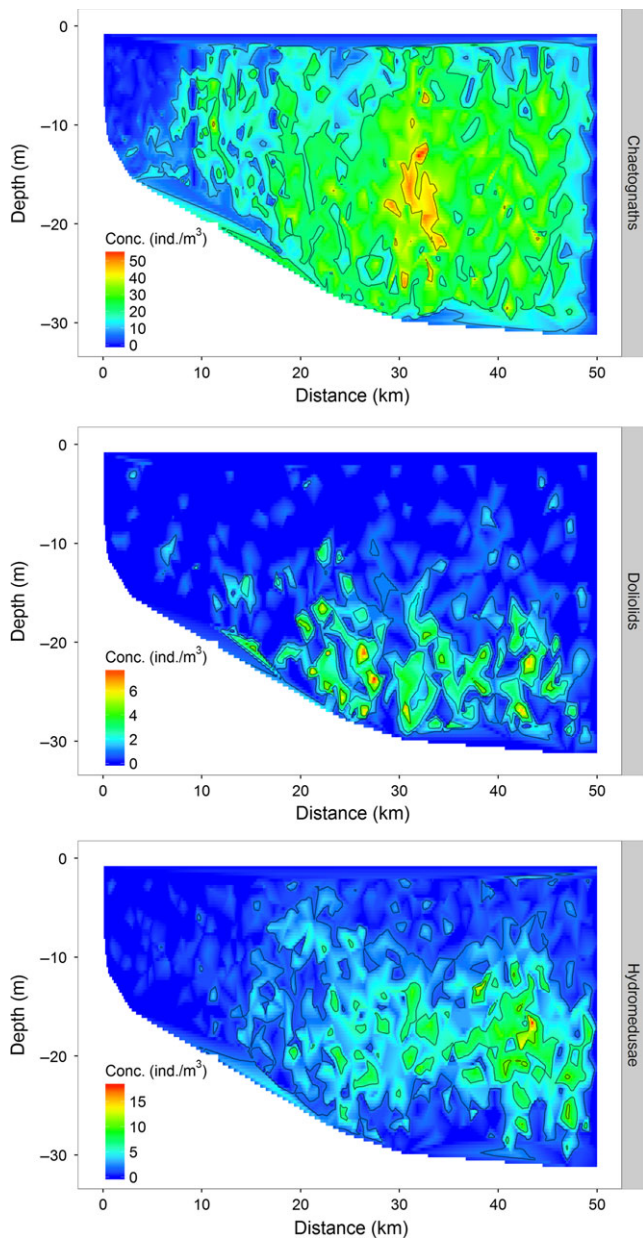
FIGURE 7 Interpolated zooplankton concentrations (ind./m³) for three taxonomic groups on October 30. Distributions are shown for chaetognaths, doliolids, and hydromedusae. Note the change in the color bar range among the different panels

1981; Yeung & McGowan, 1991). Although the phyllosoma were found in all portions of the water column, sampling on the full diel cycle would be required to demonstrate the absence of diel vertical migrations on the northern Gulf of Mexico shelf.

Our observations showed that phyllosoma were consistently oriented in a head-down posture, regardless of whether or not they were attached to a jelly. The eye anatomy of the phyllosoma (spindle-shaped rhabdom) suggests a sensitivity to polarized light (Mishra, Jeffs, & Meyer-Rochow, 2006), which can enhance contrast for detecting predators and prey (Goddard & Forward, 1991; Shashar, Rutledge, & Cronin, 1996). Further examination of the light environment (upwelling and downwelling) surrounding these

phyllosoma could explain why they consistently orient in a head-down posture. When a phyllosoma had a jelly in its grasp, it was almost always attached to the bell and positioned far from the phyllosoma mouthparts, using their 5th pereiopods (Wakabayashi, Sato, Hirai, & Tanaka, 2012). Behavioral observations have depicted phyllosoma pulling their gelatinous "host" through the water once they have become attached (Ates, Lindsay, & Sekiguchi, 2007), indicating that the phyllosoma swimming is not eliminated by the attachment to a gelatinous organism, but the attachment could influence swimming speed or response to currents by altering drag or buoyancy. Once phyllosoma vertical behavior and the fluid mechanics surrounding the larvae are more accurately described, dispersal models should incorporate this information to more accurately simulate their movements in response to current changes and the alterations of drag induced by the attachment to gelatinous zooplankton, which may be size-dependent.

The fact that the positioning of the gelatinous organisms in relation to the phyllosoma was so consistent is evidence that the data presented here show true attachment - not simply spatial overlap as an artifact of imaging a three-dimensional water parcel in two-dimensions, as is required when using shadowgraph imagery. If we assume the maximum concentration of hydromedusae detected (~15 ind./m³) was found throughout the transects, that means only 12% of the image frames would contain a hydromedusa (assuming no frames have multiple individual hydromedusae, which is not true). Within a given image, an average 8 mm individual phyllosoma only occupies 0.2% of the image (each image has a 13 × 13 cm field of view). So the probability of a relatively rare hydromedusa, and an even rarer phyllosoma co-occurring and perfectly overlapping with the end of the phyllosoma pereiopods in the same image 30% of the time is extremely small, almost certainly not occurring at random. If the jellies were much more abundant, for example, equivalent to the abundance of marine snow, we would not be as confident in the interpretation of a true attachment by the phyllosoma.

A potential shortcoming of this study, and data from towed instruments in general, is that we only have a snapshot of the phyllosoma interactions with jellies, with no information on the temporal extent of the phyllosoma attachment. Although laboratory observations have noted that phyllosoma remain attached until the entire gelatinous "host" is consumed (Wakabayashi, Sato, Hirai, & Tanaka, 2012), the extent to which this behavior may change in the natural habitat of the phyllosoma is critical for determining the type of ecological interaction and its population level impact.

4.2 | Benefits for food acquisition and protection

The most obvious and well recognized benefit to a phyllosoma attached to a gelatinous organism is that the "host" can serve as a food source, which is supported by multiple lines of evidence. First, aquaculture research has demonstrated that phyllosoma from the family Scyllaridae can be reared exclusively on a gelatinous zooplankton diet composed of tissue from a variety of species, including

venomous ones (Kittaka, 2000; Wakabayashi et al., 2012, 2016). Phyllosoma gut and appendage morphology (sharp dactyls at the ends of their pereiopods) suggests that they rely on gelatinous food or detritus and are adapted to attach to gelatinous zooplankton (Wakabayashi, Sato, Hirai, & Tanaka, 2012). A third line of evidence comes from diet studies using genetic information derived from the mid-gut of both Scyllarid and Palinurid phyllosoma, suggesting that they primarily consume gelatinous tissue from both cnidarians and urochordates (appendicularians, salps, and doliolids) (O'Rorke et al., 2015; Suzuki, Murakami, Takeyama, & Chow, 2006). We also imaged larger medusae (*Liriope* spp.) with attached phyllosoma and missing tentacles, which suggests that they had been consumed by the phyllosoma and would be consistent with laboratory observations (Shojima, 1963; Wakabayashi, Sato, Hirai, & Tanaka, 2012).

The phyllosoma association with jellies may also allow access to other prey items in higher concentrations. Phyllosoma could prey on larval fishes that use jellies as protection (Lynam & Brierley, 2007) or on microplankton stunned by nematocysts (Phillips, Burke, & Keener, 1969). Fishes have been detected in the guts of phyllosoma through genetic analyses (O'Rorke et al., 2015), and phyllosoma have been cultured in the laboratory on a diet consisting entirely of goby larvae (Dotsu, Seno, & Inoue, 1966). Better resolution of the prey preferences of phyllosoma, and whether or not it changes due to jelly attachment, will provide insight into how the jelly-phyllosoma association could improve larval survival.

Protection from predators may be an additional ecological benefit of the phyllosoma-jelly association. While it is certainly true that gelatinous zooplankton have predators (Arai, 2005; Cardona, Alvarez de Quevedo, Borrell, & Aguilar, 2012), common zooplanktivorous fishes tend to not prefer or even avoid gelatinous zooplankton (Bullard & Hay, 2002). The widespread use of Batesian mimicry by larval fishes resembling less palable gelatinous zooplankton suggests these morphologies and behaviors have benefits for avoiding visual predation (Greer, Woodson, Guigand, & Cowen, 2016). Although phyllosoma have converged on the strategy of transparency similar to gelatinous zooplankton (Johnsen, 2014), they have hard structures, so they would likely have a high caloric or carbon content relative to gelatinous zooplankton (Kiørboe, 2013), making them desirable prey for visual predators such as fish (Bailey & Habib, 1982). An alternative strategy to avoid predation would be to maintain transparency but also associate with a transparent and less palatable organism, thereby improving their mode of crypsis by adding a level of avoidance; predators will see an undesirable prey item (with attached phyllosoma) and potentially avoid making a close approach. It seems likely that the phyllosoma-jelly interaction may involve some degree of predation protection by associating with a less palatable animal. This benefit, of course, would depend on the size of the jelly relative to the phyllosoma, the visual acuity of an approaching predator, and its prey preferences. The cost of the association with gelatinous zooplankton is that the phyllosoma are exposed to fouling by mucus secreted by some jellies (Niggl, Naumann, Struck, Manasrah, & Wild, 2010; Shanks & Graham, 1988) and must continuously groom using their third maxilliped (Kamio et al., 2015). The degree to which

potential benefits of predation protection or feeding contribute to phyllosoma survival requires further study.

Imaging systems provide an ideal tool to examine ecological interactions in the plankton, but these data alone do not tell the whole story. While we were able to discern the frequency of the phyllosoma interactions with a variety of gelatinous zooplankton groups and some potential biological and physical drivers of this relationship, only through increasing use of imaging systems in combination with diet studies and broader scale observations of larval condition and recruitment will we be able to determine the population level impact of these species interactions. Further laboratory analysis may reveal precise details on the conditions leading to certain behaviors of the phyllosoma, which would allow scientists to accurately classify the phyllosoma-jelly interaction and determine its potential impacts on population level processes. Once species interactions are described, then fisheries managers can use data related to the abundances of these taxa, in combination with oceanographic conditions, to better predict population dynamics of commercially important species with complex life histories.

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