



Food for Thought

From spatial pattern to ecological process through imaging zooplankton interactions

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Ecological interactions among marine zooplankton are poorly described because conventional sampling gears, such as plankton nets and traps, obscure the physical and biological environment that individuals experience. With *in situ* imagery, however, it is possible to resolve these interactions and potentially convert snapshot distributions into process-oriented oceanographic and ecological understanding. We describe a variety of imagery-detected ecological interactions with high spatial resolution in the northern Gulf of Mexico shelf waters (20–35 m bottom depth), providing new evidence of parasitism, predation, and life stage spatial structuring for different zooplankton groups. Chaetognaths were infected with an anteriorly attached, parasitic polychaete (1.1% of 33 824 individuals), and these infected chaetognaths were more common further offshore, south of a nearshore patch where unparasitized individuals reached concentrations of $\sim 90 \text{ m}^{-3}$. Predation by *Liriope* spp. hydromedusae tended to occur in the shallowest 10–15 m, and doliolids formed distinct patches of different life stages, indicating that the environment is replete with sharp transitions among various ecological processes. Similar patterns in other marine ecosystems likely exist, and we encourage hybrid (machine/human expertise) approaches that broaden the scope for analysis of plankton images, which are rich sources of new ecological information and hypotheses yet to be examined quantitatively.

Keywords: Chaetognath, commensalism, doliolid, gelatinous zooplankton, *in situ* imagery, larval fish, life history, parasitism, predation

Introduction

Marine ecosystems contain a variety of interacting organisms, and a key to understanding how ecosystems operate in a steady state and respond to perturbations (both large scale climate and more acute changes) lies in understanding the details and consequences of ecological interactions (Lawton, 1999). Defined here as the sharing of habitat space between individuals that likely has a fitness cost or benefit, ecological interactions can be examined through experimental manipulation or direct measurements, such as gut content analysis (i.e. through microscopy or genetics to measure predation and diets, Walters *et al.*, 2019; Axler *et al.*, 2020). Indirect meth-

ods can also be used to detected ecological interactions, which include describing the co-occurrence of species (Blanchet *et al.*, 2020) or spatial overlap among known predators and prey (Benoit-Bird and McManus, 2012; Greer and Woodson, 2016; Swieca *et al.*, 2020; Axler *et al.*, 2020) or competitors (Brodeur *et al.*, 2008). These studies of shared habitat and spatial overlap, while useful for understanding ecological processes (Carroll *et al.*, 2019), typically assume that shared space indicates interaction.

Marine zooplankton display complex behaviours, life histories, and ecological strategies, implying that spatial overlap alone does not necessarily indicate that interactions are occurring (Blanchet *et al.*, 2020). Conventional sampling gears (e.g. plankton nets)

have taxonomic biases favouring crustaceans and generally produce data that average large swaths of the water column (10s of meters). With these sampling methods, fine-scale spatial relationships cannot be detected, so organisms that appear in a single net tow may not occupy similar water masses. Plankton net tows, therefore, are not appropriate for describing many ecological interactions at fine spatial scales, especially if artefacts from net-feeding are not taken into account (Fuentes and Quiroga, 2012). Studies utilizing *in situ* imaging systems are revealing fine-scale vertical and horizontal structure in a variety of marine environments, with the typical aim of quantifying the abundance of different taxa, either through manual or semi-automated image analysis (e.g. Luo *et al.*, 2018; Ellen *et al.*, 2019; Briseño-Avena *et al.*, 2020). Although these studies describe community composition, spatial relationships, and associated oceanographic parameters, there is potentially more information available within the images that can be useful for understanding plankton ecology, such as interactions with potential food sources (Möller *et al.*, 2012; Greer *et al.*, 2017), conspecifics or commensal organisms (Greer *et al.*, 2018a), parasites (Peacock *et al.* 2014), and life stage, morphology, or health status (Baumgartner *et al.*, 2011; Takahashi *et al.*, 2015; Kenitz *et al.*, 2020).

In situ imaging can provide direct evidence of interactions at the time of sampling and in the recent past, but methods of processing and interpreting these data are still in their infancy, primarily due to the volume of data and the difficulty of detecting interactions automatically. Details of interactions depicted within the images tend to be ignored or treated as anomalies in automated processing pipelines—and for good reason. Considering the steps needed to automate plankton image processing for a variety of taxa, images showing ecological interactions will differ substantially from “representative” images (i.e. one individual per region of interest) that tend to populate the image recognition training library. It is therefore unclear how to design a robust method for extracting and understanding interactions in an automated fashion. Even if the individuals participating in the interactions are accurately classified, current deep learning algorithms cannot “understand,” in our sense of the word, quantitatively ascribe purpose, or assess the meaning of spatial relationships within an image—a task that our human brains are extremely skilled at performing (Marcus, 2018). Because these interactions are likely spatially heterogeneous, automated recognition that mistakenly omits or misidentifies these interactions also risks losing information that highlights key ecological processes influencing the water masses before they were sampled.

The goals of this study were to (1) describe several examples of ecological interactions in the context of oceanographic processes using *in situ* imagery and (2) inspire researchers in biological oceanography and trophic ecology to use imagery to augment studies of co-occurrence, diets, and other interactions. Not only are *in situ* plankton images showing us that the ocean is a “sea of tentacles” (Ohman, 2019), they also depict a sea of interactions—many of which we are only beginning to describe but may have profound implications for our understanding of marine ecosystem functioning. While this study focuses on examples from the northern Gulf of Mexico, colloquially known as a “fishy sea” due to its high biological productivity (Davis, 2017), similar interactions are likely occurring in other marine ecosystems that have not been as extensively sampled with *in situ* imagery.

Methods

The *In Situ* Ichthyoplankton Imaging System (ISIIS) is a towed underwater vehicle that captures images of plankton between $\sim 500\ \mu\text{m}$ and 12 cm in size (~ 60 micron pixel resolution), generally preserving their natural orientation and spatial relationships (Cowen and Guigand, 2008). There are exceptions for highly motile and larger plankton, such as euphausiids, which may not have their natural orientation preserved since they are often engaging in an escape response when imaged. The images are collected using a shadowgraph lighting technique, which projects a light source across an imaged water parcel (field of view: 12 cm, depth of field: 50 cm), and the plankton or particles that block the light source are captured by the line scan camera as a shadow. Recording software parses the imagery into square 12 cm x 12 cm frames, but the system samples a continuous strip of ocean along its towed path. Shadowgraph imagery allows for all particles within the imaged water volume to remain in focus, so organisms that appear to overlap in the 2D images can be as far apart as 50 cm (the length of the depth of field). For this reason, additional evidence besides simple overlap in the image, such as outstretched tentacles (anomalously positioned relative to others) or probabilities based on abundance (e.g. Greer *et al.*, 2017), must be present to determine with confidence that an interaction is taking place. The ISIIS is towed at a horizontal speed of $2.5\ \text{m s}^{-1}$ and moves vertically throughout the water column (near surface to $\sim 2\ \text{m}$ from the bottom) at $0.2\text{--}0.3\ \text{m s}^{-1}$. The system is equipped with several oceanographic sensors, including a CTD (SBE 49 Fast-CAT) and chlorophyll-*a* fluorescence (Wetlabs ECO FL-RT), that collect data at $\sim 8\ \text{Hz}$.

Imagery data were obtained during the summer of 2016 as part of a three-season survey in the northern Gulf of Mexico, with sampling transects encompassing a $\sim 6\ \text{hr}$ period, centred around noon local time (Greer *et al.*, 2018b). The images were processed for a $\sim 50\ \text{km}$ transect conducted on 26 July 2016 just south of Perdido Bay, FL following a series of steps similar to those detailed in Greer *et al.* (2018a), which resulted in extracted regions of interest (ROIs) above a 2000-pixel size threshold ($\sim 3.3\ \text{mm}$ equivalent spherical diameter). The ROIs were manually classified to broad taxonomic categories (e.g. hydromedusae, siphonophores, chaetognaths, etc.), and gelatinous zooplankton were further classified to genus or species level or life stage where appropriate. For doliolids, they were classified as phorozooids/gonozooids or nurses depending on the presence of a cadophore (the long tail-like feature on the nurse stage of doliolids).

For several relatively abundant groups, the occupied oceanographic environments were compared between individuals engaging or not engaging in an ecological interaction. Each image classified as a *Liriope* spp. medusa (534 individuals) was further categorized as “no interaction,” “eating” (prey visible in the manubrium), “parasites” (if parasites present on the bell), or “spent” (if gonads were visibly empty or “spent”). To test for depth differences between feeding *Liriope* spp. and individuals not engaging in an interaction, a bootstrapping procedure was used. From both the feeding and non-interacting populations, a random sample of the number of feeding medusae imaged (76) was extracted with replacement. The mean depth was then calculated for each group, and this process was repeated for 10 000 trials. The differences between the mean depths was computed for each trial, and the *p* value was assessed by the percentage of times the mean depth was deeper for the feeding vs. non feeding individuals. No other statistical tests were performed for the other interactions types because the sam-

ple sizes were much lower relative to the feeding *Liriope* spp. The much more abundant chaetognaths (33 824 individuals) were examined to determine whether or not they had visible, external parasites. Each individual chaetognath was merged to its nearest fine-scale environmental parameters, and the differences in depth occupied, salinity, temperature, latitude, and chlorophyll-*a* fluorescence between infected vs. non-infected individuals were assessed using a similar procedure described above for *Liriope* spp. but drawing 376 individuals randomly (with replacement) from each group. Abundances of chaetognaths and doliolids were binned by 1 m³ (~17- and 1.4-m horizontal and vertical distance, respectively, traveled by the ISIIIS) to generate fine-scale concentrations and linearly interpolated across the entire transect to compare to the location of the doliolid life stages and chaetognath interactions with parasites. This bin size was chosen for convenience since counts are also concentrations (number m⁻³), but it also balances the tradeoff between sample volume and vertical resolution for calculating accurate fine-scale concentrations and proportions of those groups engaging in interactions, when appropriate. Other individual examples of interactions were acquired from the entire field sampling campaign in the northern Gulf of Mexico (Greer *et al.*, 2018b).

Results

Several types of ecological interactions were detected with *in situ* imagery—all in relation to the fine-scale physical oceanographic environment. These interactions were either direct—meaning that at least two organisms were spatially co-located, making physical contact, or a single organism had evidence of a recent interaction—or the interactions were related to life history, where the life stage was classified to indicate the growth status of the population.

Direct ecological interactions and behaviour

Because *in situ* imaging produces data on fine spatial scales, it allows for unprecedented descriptions of how organisms share space in the water column. For example, there is potential for competition in situations where 32 larval fishes occupy a 7200 cm³ parcel of water (Figure 1a). Direct evidence of competition (or possible cannibalism) can be seen in examples of chaetognaths that appear to be locking jaws (Figure 1b–d). Several taxa harboured parasites, such as chaetognaths with polychaetes (Figure 1e) that sometimes appeared to devour their heads (Figure 1f), and salps parasitized by hyperiid amphipods (Figure 1g) or crustaceans (Figure 1h).

Some of these direct interactions can be interpreted as predation events. Chaetognaths were imaged preying upon larval fishes not much smaller than themselves (Figure 1i). Hydromedusae showed conspicuous evidence of predation and were sometimes depicted consuming marine snow or other zooplankton (Figure 1j). Body damage to individual zooplankton indicated recent narrowly escaped predation or competitive interactions (Figure 1k).

Other interactions provided clues about different strategies organisms use to survive in the plankton. Imaging revealed close associations that had an unclear fitness cost or benefit to the participants, which we categorized as commensalism. Larval and juvenile fish can closely associate with a variety of gelatinous organisms, including siphonophores (Figure 1l), hydromedusae, and pelagic tunicates, as well as larval tube anemones (Figure 1m). This interaction potentially benefitted the larva by protecting it from predation through associating with an organism that has stinging nematocysts, yet there may be risks to this association as well. In other cir-

cumstances, however, the fitness benefit for the fish may be acquired through mimicry (flatfish larva that appears to swim behind a large salp chain; Figure 1n). Other behaviours associated with swimming can be seen in the images. Patches of different (shrimp and fish larva, Figure 2a) or similar taxa (Figure 2b–d) sometimes mirror one another, potentially indicating similar responses to stimuli. In some cases (e.g. Figure 2a and d), the passing imaging system could induce similar escape responses, and the images can indicate salp chains swim in a cork-screw pattern (Figure 2e).

Life history traits and reproduction

Life history characteristics can be thought of as a lagging indicator of past ecological interactions. Not only can the size and reproductive status of some organisms be established, but for organisms with particular orientations, the number of vertebrae or other meristics (e.g. fin ray counts) can be used to approximate the age or the genus/species-level identification of the imaged individual. For instance, moon jellies (*Aurelia* spp.) were seen in different developmental stages (Figure 2f and g), and branching points in the gastrovascular system of juveniles can serve as a proxy of relative age (Chiaverano *et al.*, 2016). The images also showed developmental abnormalities (Figure 2h, normal–4 c-shaped gonads and 4 oral arms and Figure 2i, abnormal–3 gonads and 2 oral arms), and reproductive events were documented in salps (Figure 2j).

Oceanographic context of ecological interactions

Distributions of different life stages can indicate which parts of the water column are associated with population growth. All doliolids life stages were closely associated with the strong pycnocline at ~10 m. Doliolid nurses, however, were generally confined to nearshore waters (5065 individuals, Figure 3a), while doliolid phorozoids and gonozoids (20 896 individuals) were densely aggregated further offshore, reaching peak abundances that were an order of magnitude higher than the nurses (Figure 3b). The phorozoid/gonozoid stages were almost completely absent from waters below the pycnocline, which contained relatively low abundances of doliolid nurses closer to shore.

Gelatinous zooplankton, due to their transparency, offer many opportunities to document several types of ecological interactions not possible to see *in situ* with more opaque (e.g. crustacean) zooplankton. *Liriope* spp. hydromedusae tended to be most abundant near the surface and along the bottom, with a dense aggregation near a surface salinity front at ~20 km along the transect (Figure 4a). The location of their interactions, however, were generally confined to specific portions of the water column. Most of the *Liriope* spp. individuals that were consuming prey were found in the shallowest 15 m (78.9%), occupying significantly shallower depths compared to ones that were not engaging in an interaction ($p = 0.002$) (Figure 4b). Individuals that were infected with at least one parasite (likely hyperiid amphipods) occurred in small patches at various parts of the transect but generally resided in the upper water column (Figure 4c). Individuals with spent gonads were exclusively seen on the southern end of the transects in both the surface and bottom waters (Figure 4d).

Chaetognaths harboured an ectoparasite (1.1% of 33 824 individuals), and their abundance allowed for the quantification of apparently infected/non-infected individuals, as well as their respective associations with fine-scale oceanographic habitat. The parasite was identified as a typhloscolecoid polychaete and was always

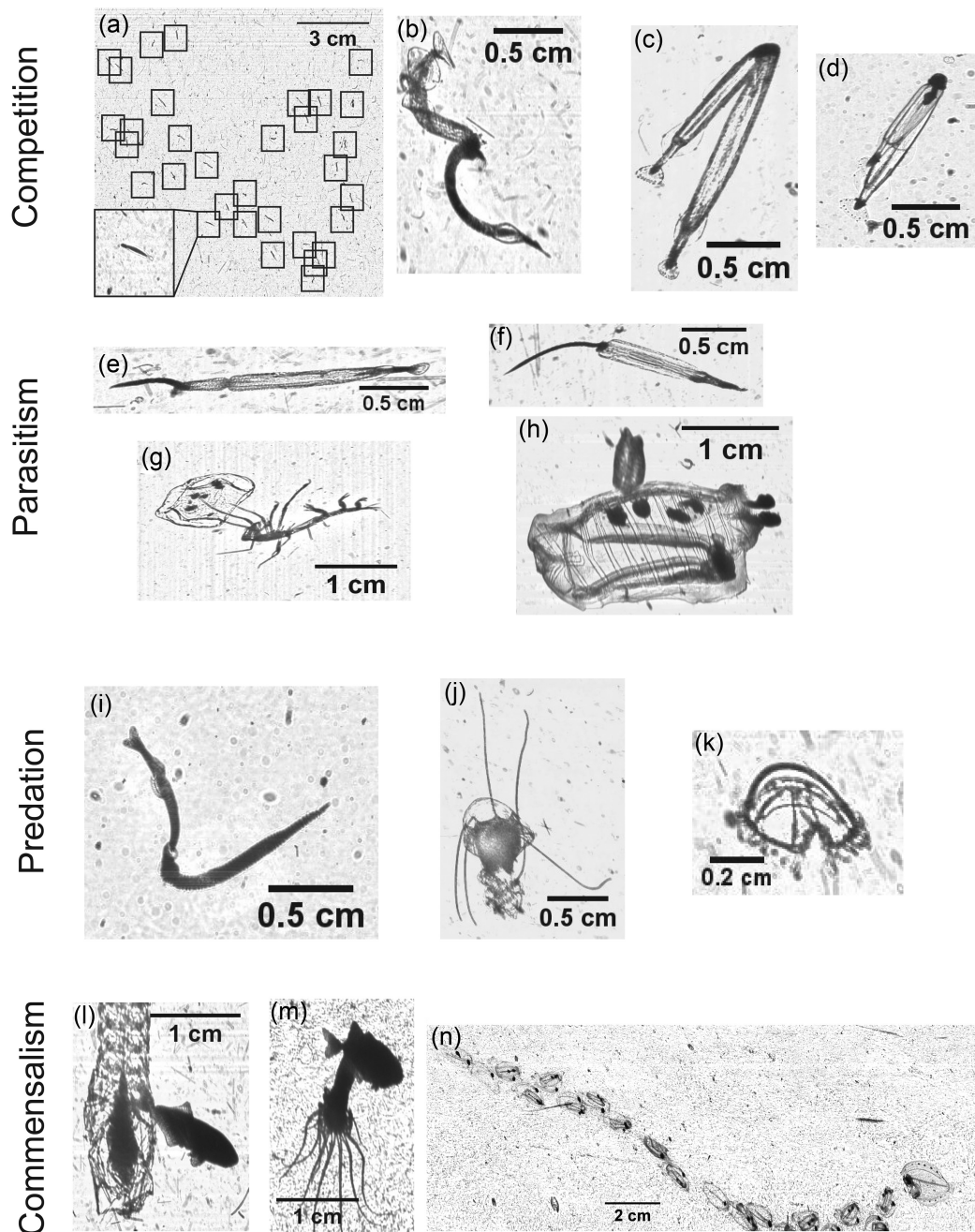


Figure 1. Examples of direct ecological interactions depicted with *in situ* imagery: Panel (a) 32 individual larval fish (indicated by the boxes) potentially competing for small scale resources. One individual is duplicated in the bottom left corner as a larger size for easier visualization. Panel (b)–(d) chaetognaths with their mouths locked—possibly engaging in some form of competition, Panel (e–f) chaetognaths harbouring a parasitic polychaete, Panel (g) salp parasitized by a hyperiid amphipod, Panel (h) salp harbouring crustacean parasites, Panel (i) chaetognath (below) consuming a larval fish (above), Panel (j) hydromedusa consuming marine snow, Panel (k) evidence of recent interaction in a hydromedusa (body damage), and larval fishes closely associating with a Panel (l) siphonophore, Panel (m) tube anemone larva, and Panel (n) salp chain.

found attached to the chaetognath's head-region. In certain images, the parasite appeared to have consumed the anterior portion of the chaetognath. The species-level identification of this parasite is unclear, but it appears to be common during the summer months in the northern Gulf of Mexico, although the free-swimming abundance of this polychaete was not quantified. Even though chaetog-

naths reached high concentrations ($\sim 90 \text{ ind. m}^{-3}$) on the northern end of the transect, most of the infected individuals were not present in this area (Figure 5a). Instead, higher proportions of infected chaetognaths tended to occur when abundances were low in water masses $> 10 \text{ m}$ deep (Figure 5b) that tended to be further offshore (lower latitudes) with lower temperatures and higher salini-

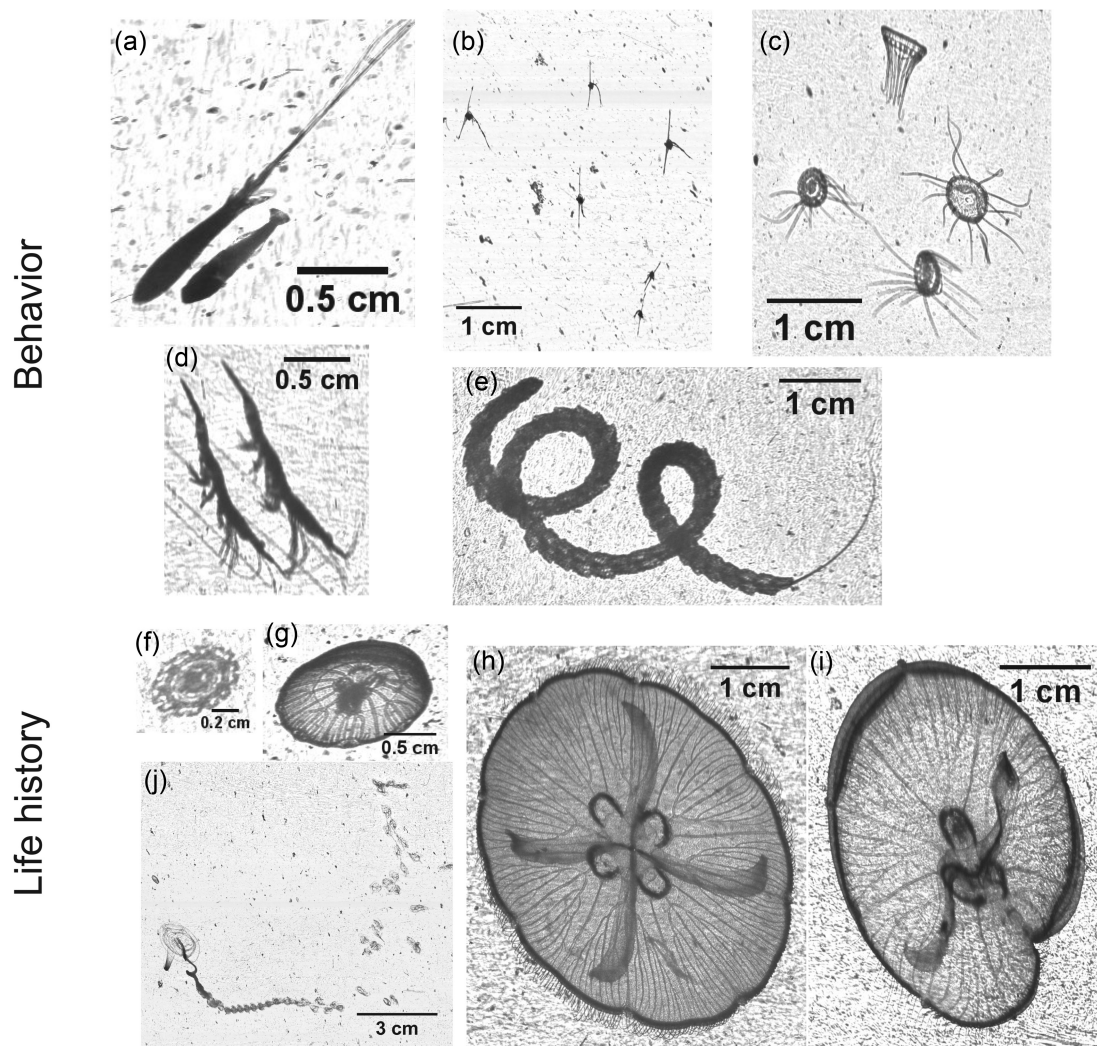


Figure 2. Examples of behavioural interactions and life history traits from *in situ* imagery: Similar orientations for Panel (a) shrimp (curled up in swimming posture, above) and larval fish (below), Panel (b) six crab zoeae, Panel (c) *Solmaris* spp. medusae, and Panel (d) two shrimps, Panel (e) salp chain in a coordinated spiral for locomotion, Panel (f) ephyra of a scyphomedusae, Panel (g) juvenile moon jelly (*Aurelia* spp.), Panel (h) normal juvenile moon jelly, Panel (i) juvenile moon jelly with developmental abnormality (two visible oral arms and three gonads instead of four), Panel (j) salp in the midst of producing a chain of individuals, while also likely being broken apart by the passing imaging system.

ties (Figure 5c). There was no significant difference in depth occupied or relative chlorophyll-*a* fluorescence ($p > 0.001$) for infected vs. non-infected chaetognaths.

Discussion

In situ imagery provides a rare glimpse into the experience of individual organisms, ecological interactions, and tradeoffs they must navigate within their heterogeneous ocean habitat. Here, we demonstrate that imagery provides evidence, either instantaneous or from the recent past, of a wide range of ecological interactions. All of these interactions can be interpreted in the context of the oceanographic conditions and shine a light onto a new scientific landscape replete with potential discoveries, particularly given the promise of accelerating development of automated image processing.

Oceanographic context of parasitism, predation, and life stage

The role of parasites in controlling population dynamics, and how this connects to oceanography, can be explored through *in situ* imagery. Similar typhloscolecoid polychaetes have been detected on chaetognaths (Feigenbaum, 1979) and had infection or decapitation rates, quantified with net samples, between 0.2 and 5% in various locations (Øresland and Bray, 2005). In the case of parasitism, where the interaction is sustained through physical attachment, we would expect to see similar rates of infection to those detected in plankton nets, which was indeed the case in the imagery (1.1% of chaetognaths infected). Use of microscopy to quantify parasitism in chaetognaths allows for detecting much smaller forms of the parasite than is possible with imagery, yet this method requires preserved specimens and extensive microscope sorting, with the additional possibility of chaetognath heads being lost through damage or predation in the plankton net and cod end. Images, how-

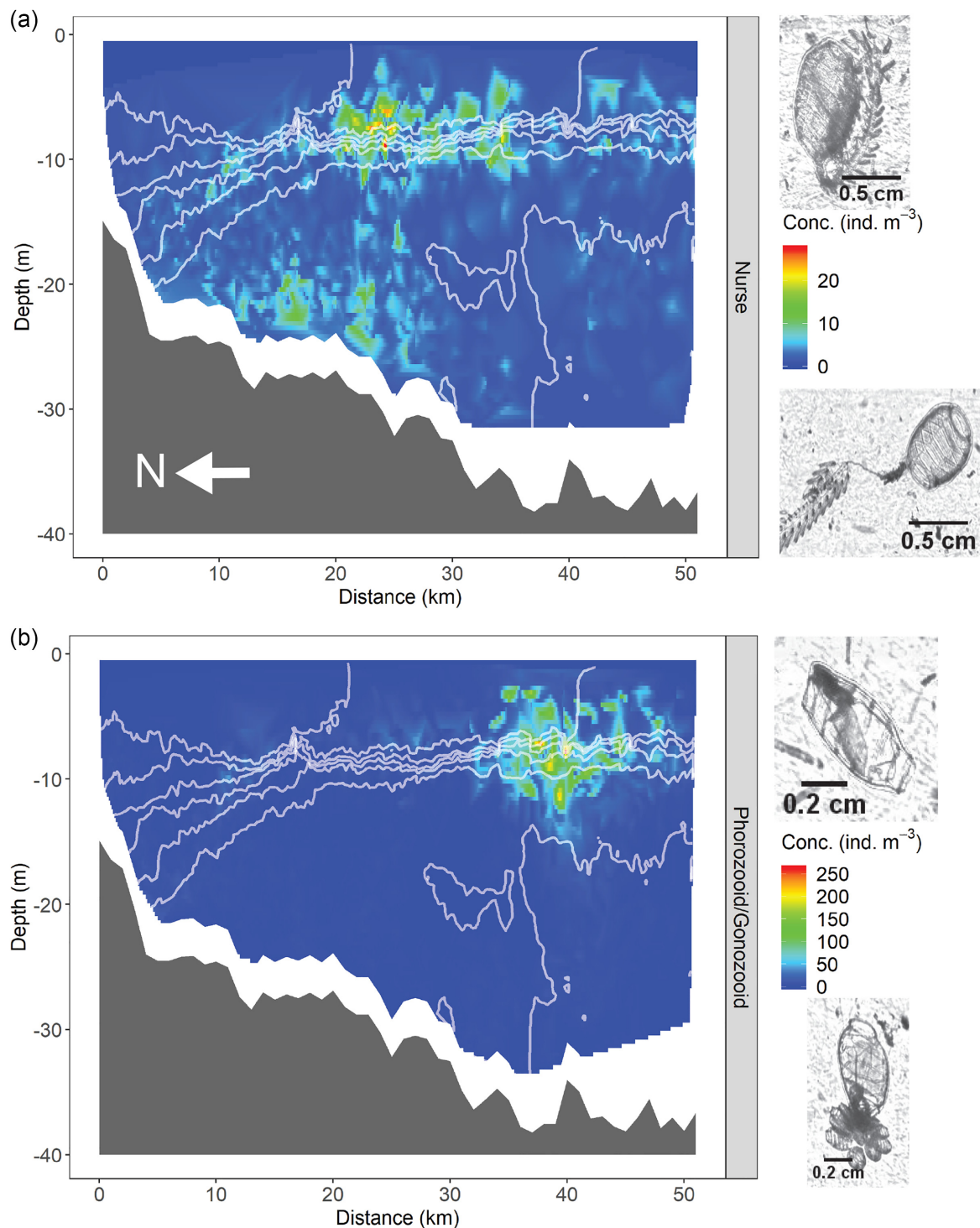


Figure 3. Life stage-specific distribution of doliolids in relation to isohalines (30–36, white lines) for Panel (a) nurses and Panel (b) phorozoids/gonozoids. The dark gray polygon denotes the trajectory of the benthos.

ever, could theoretically be classified quickly with a trained algorithm and used to complement more detailed analyses of infected *vs.* non-infected individuals, as well as provide precise locations and multiple corresponding oceanographic parameters for these observations. Indeed, the infected individuals had significantly different oceanographic habitats (lower latitudes, lower tem-

peratures, and higher salinities) compared to non-infected individuals, which tended to reside nearshore. Similar spatial patterns of parasitism likely exist in other ecosystems where *in situ* imaging technology has not been regularly deployed. Our results suggest parasitism is more likely in non-optimal habitat, as chaetognaths south of the main aggregation were more commonly harbour-

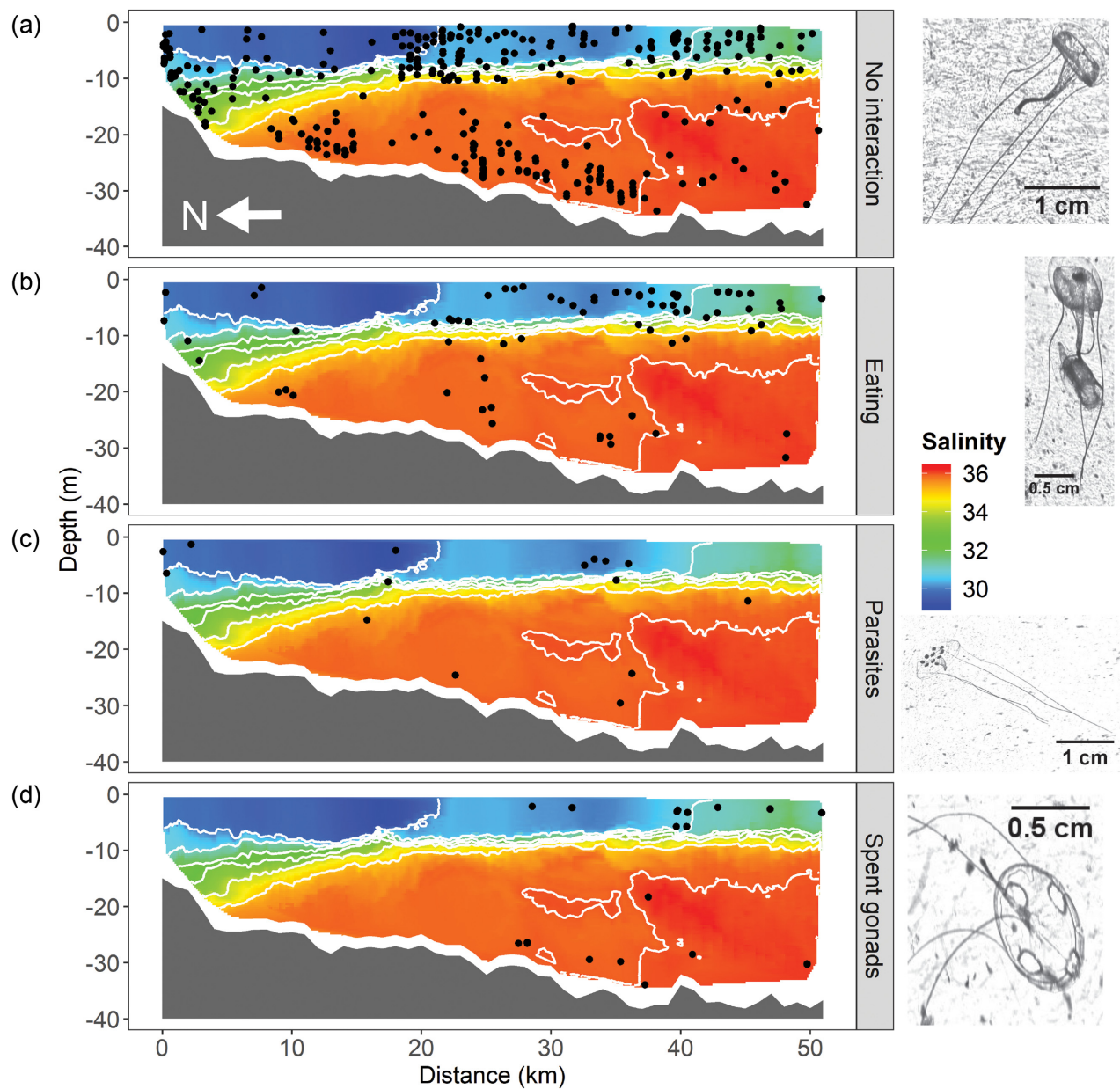


Figure 4. Location of *Liriope* spp. interactions along the transect for Panel (a) no interaction detected, Panel (b) individuals consuming prey, Panel (c) infected with a parasite, and Panel (d) individuals with spent gonads. White contours correspond to isohalines 30–36, and the dark gray polygon depicts the trajectory of the benthos.

ing visible parasites. Alternatively, parasitism could reduce swimming capabilities, causing infected chaetognaths residing below the pycnocline to be swept further offshore, as would happen during the downwelling event observed in this study (Dzwonkowski *et al.*, 2018).

Liriope spp. hydromedusae were found throughout the water column, yet their ecological interactions showed varying spatial patterns. Predation tended to occur near the surface, while the distribution of *Liriope* spp. with spent gonads and parasitic infections did not show a clear spatial pattern. This may indicate that healthier, feeding individuals reside in the surface, but measurements of nutritional condition would be required to determine this conclu-

sively. The widespread distribution of *Liriope* spp. and some association with surface changes in salinity is consistent with another study showing that they tolerate a wide range of oxygen concentrations and associate with fronts (Pavez *et al.*, 2010). However, our observations are some of the first to describe their interactions with other organisms. *In situ* imagery has potential for major advances in ecological knowledge due to the fact that reproductive status and feeding can be documented on fine scales for *Liriope* spp. and similar gelatinous species.

Doliolids are gelatinous organisms capable of quickly forming massive blooms that are difficult to predict (Deibel and Paffenhöfer, 2009). Quantifying abundances in relation to life stages

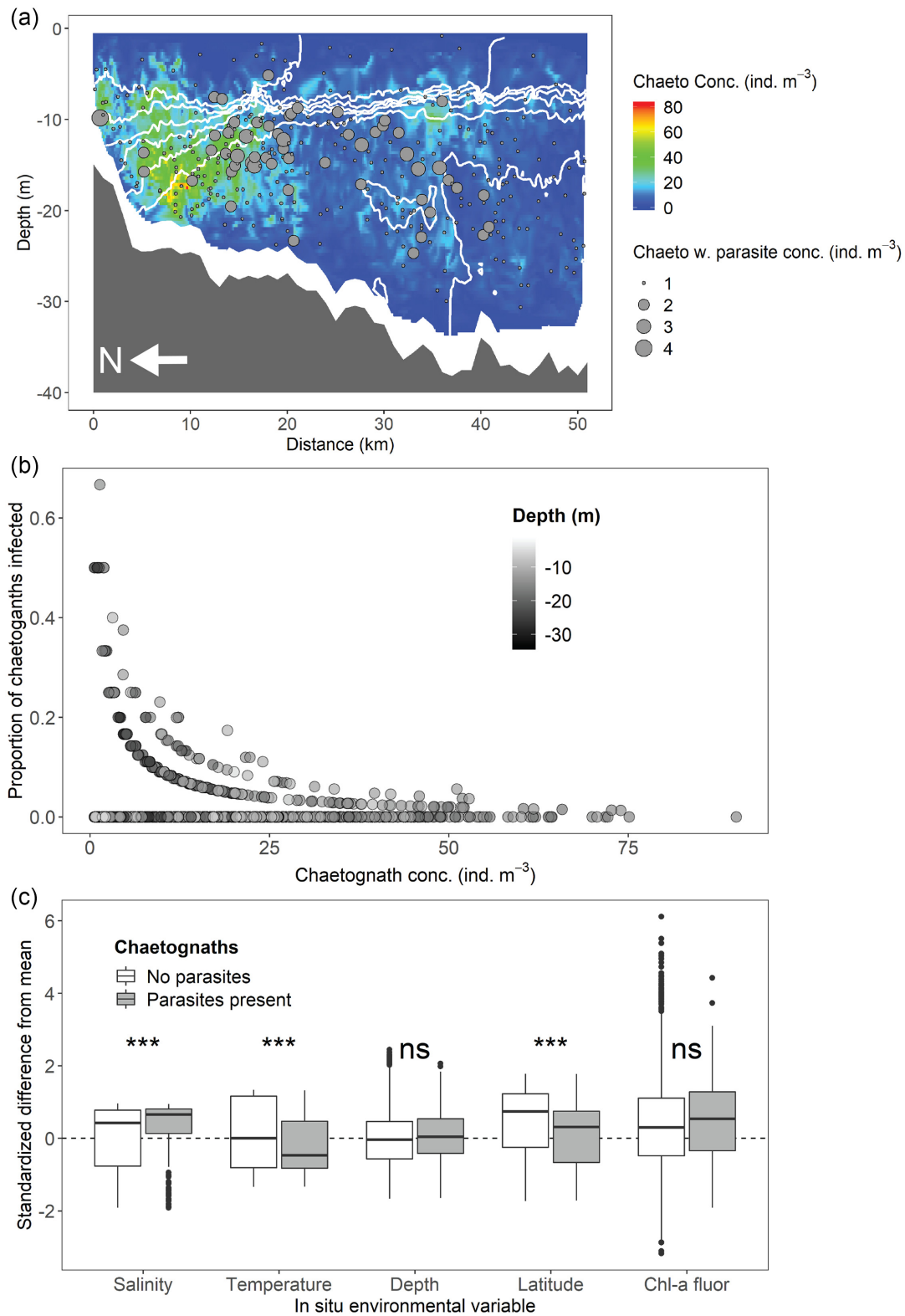


Figure 5. Panel (a) Fine-scale concentration of chaetognaths with and without visible, attached parasites. White lines indicate isohalines 30–36. Panel (b) Fine-scale abundance of chaetognaths vs. the proportion infected by parasites. Colour of the dot indicates the mean depth location for each calculation (1 m^3 bin). Panel (c) boxplots showing standardized habitat associations for chaetognaths with and without attached parasites. Statistical significance of differences in mean between each group is indicated by the following: “ns” for $p > 0.001$, “***” for $p < 1\text{e-}6$. The dotted line at zero refers to the mean value for each oceanographic parameter measured across the entire transect.

and oceanography, therefore, is key for determining the mechanisms driving these blooms. Although all doliolids tended to aggregate along the pycnocline, an area where marine snow aggregates are concentrated during the summertime (Greer *et al.*, 2018b), patches of doliolids were dominated by specific life stages that were horizontally separate. The patch towards the southern end of the transect had higher abundances and contained mostly the phorozoid/gonozoid stages, which indicate a relatively recent asexual reproduction event (Deibel and Paffenhöfer, 2009; Walters *et al.*, 2019). These same life stages dominated a thin layer of phytoplankton described during this field sampling campaign, although the thin layer had doliolid abundances >2 orders of magnitude higher and was found further towards the west (Greer *et al.*, 2020). Near the Kuroshio Current, doliolids also formed life stage-specific patches, and nurse abundance was negatively correlated with total abundance of doliolids, or in other words, spatially separated from the site of a recent bloom (Takahashi *et al.* 2015). These results suggest that particular microhabitats are favorable for blooms of doliolids, and similar processes could be found for other gelatinous zooplankton whose spatial patterns have not been described in detail.

Computer science to the rescue, a call for wider engagement, or both?

The staggering amount of data produced by imaging systems like the ISIS (up to 7.2 GB min⁻¹ or millions to billions of ROIs from a ~1-week research cruise, depending on the ecosystem) creates strong incentive to completely embrace fully automated analysis. A fundamental first step, however, is to determine the scientific capabilities of *in situ* imaging systems, requiring ecological expertise along with a critical evaluation of these instruments for addressing different scientific questions. Although design of various semi- or fully-automated image processing procedures is already underway or completed, our results demonstrate that we will limit the potential scientific impact of these data by pursuing only taxon-based classification. Despite their scientific value, the relative rarity (within the examples of different taxa), variability within, and diversity among ecological interactions makes implementing automated “deep learning” detection algorithms challenging due to the requirement of massive training sets (e.g. Luo *et al.*, 2018; Ellen *et al.*, 2019; Orenstein *et al.*, 2020), which may not be feasible if the research goal is to classify every ROI in the dataset to the lowest taxonomic level possible. However, it is also possible to fine-tune the automated classification task by using a few classes relevant to a particular phenomenon. In this case, all ROIs not targeted by the classifier will go to a “catch-all” category, and this process will produce a new dataset to study the phenomenon of interest. For example, Orenstein *et al.* (2020) successfully trained an algorithm with three categories to target a cyclopoid copepod population harbouring parasites, generating a time series with hourly resolution to study parasite-host interactions *in situ*. Results from our study imply that caution should be exercised when attempting to perform real-time automated classification because the types and extent of ecological interactions are diverse and poorly described in most ecosystems.

New approaches have been developed to incorporate citizen science into marine ecological research (Robinson *et al.*, 2017; Hardison *et al.*, 2019) that can inspire imagination and empower individuals to make new discoveries (Dolan, 2019). Recent ef-

forts have combined deep learning and citizen science for large-scale image processing and annotation (Sullivan *et al.*, 2018; Langenkämper *et al.*, 2019). To detect interactions as shown here with *in situ* plankton imagery, the annotator must have a solid understanding of both the optical mechanism generating the images and the organisms’ ecology (to determine which interactions make sense or could be artefacts of the way the images are collected). Implementing machine learning algorithms that can seamlessly receive feedback from trained citizen scientists has potential to generate many discoveries with *in situ* imaging, and this process can be augmented through spreading awareness of the array of ecological information contained in each image.

Describing ecological interactions will take *in situ* imaging beyond comparison of fine-scale snapshot distributions and into the realm of biological oceanographic processes—something that can enhance the depth and breadth of analysis for future and previously collected imagery datasets. This provides a pathway to convert inferred interactions, through either spatial overlap or co-occurrence data, to an understanding of the trophic consequences of different plankton groups sharing habitat over a certain period of time. Although new methods are being developed to efficiently detect these interactions within some acceptable degree of error (Peacock *et al.*, 2014; Orenstein *et al.*, 2020), we are just beginning to explore this new scientific frontier of how organisms interact within their dynamic oceanographic habitat.

Author contribution statement

ATG led the manuscript effort and wrote the first draft. ATG, LMC, and CBA conceived of the research question and analytical approach. FJH co-designed the field survey, and ATG and CBA collected the field data. LMC performed the initial identifications for the zooplankton images and contributed to writing and organizing the manuscript. LMT performed a literature review and wrote parts of the discussion. ATG generated the figures and analyzed the data. All co-authors contributed to editing the manuscript and helped to shape its content and design of the figures.

Data availability statement

This research was made possible by a grant from the Gulf of Mexico Research Initiative (GoMRI). All data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (doi:10.7266/N75T3HXP, 10.7266/TNP55PE8).

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