

THE VERTICAL AND HORIZONTAL DISTRIBUTION OF
BRYOZOAN LARVAE IN THE WESTERN ATLANTIC AND THE
GULF OF MEXICO

by

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A THESIS

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Title: The Vertical and Horizontal Distribution of Bryozoan Larvae in the Western Atlantic and the Gulf of Mexico

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Years of oceanographic cruises and larval collection around the Gulf of Mexico and the Western Atlantic margin revealed the prevalence of two main morphotypes of bryozoan *Cyphonautes* larvae. This thesis explores the hypothesis that these are two separate and distinct species, a hypothesis that is supported by observations of horizontal distribution, depth distribution, and morphology. Further I explore the potential life histories and areas of origin of the two morphotypes. Using distribution mapping as well as ocean particle tracking programs to create reverse trajectory models I show that morphotype 1 is likely the larva of a pseudoplanktonic bryozoan, *Jellyella sp.*, that disperses on floating algae with the circulation of the north Atlantic gyre. Morphotype 2 occurs mostly in the Gulf of Mexico, with individuals outside the Gulf associated with the Gulf Stream and the Florida Current.

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Introduction

Study Organisms: Cheliostome Bryozoans

Bryozoans are small colonial organisms that use a feeding apparatus called a lophophore to filter food out of the water column. Bryozoans can take many forms, ranging from a branching structure to an encrusting colony. Adult bryozoans are sessile, spending their adult lives attached to a substratum, whether a drifting piece of kelp (as in the case of the *sargassum* bryozoan *Jellyella tuberculata* (Bosc, 1802)), or a rock in the intertidal or subtidal zone. Most marine bryozoans on relatively shallow substrate, where wind currents and wave action provide water movement that brings food within reach of the colony (Pratt, 2008). Some bryozoans have adapted to the conditions of the deep sea, particularly near hydrothermal vents. Examples include, *Euginoma cavaleri* (Lagaaij 1963) which survives up to 2161m deep, or *Celleporaroa magnifica* (Osburne 1914), which can survive up to 2421m deep (Winston and Maturo, 2009).

Larvae and their Distributions

All bryozoans produce a free swimming planktonic larval stage. The combination of adults living a sessile life and inhabiting areas of high flow means that producing free floating larva is incredibly advantageous for bryozoans. Immediately moving offspring out of the parents' habitat decreases intraspecific competition, colonizes new areas, and increases connectivity (De Meester et al. 2015). The free swimming larval stage is likely one factor that permits many bryozoan species to achieve incredibly large distributions (Watts and Thorpe, 2006).

The majority of living marine Bryozoans fall into the class Gymnolaemata. Gymnolaemate bryozoans are known to produce three different types of larvae: cyphonautes,

pseudocyphonautes and coronate larva. The focus of this study is on cyphonautes larvae, which are characteristic of anascan cheliostome bryozoans. Anascan bryozoans are mostly thin crusts with uncalcified frontal membranes that often live on seaweed such as kelp (Bock, 1982).

Cyphonautes are weakly swimming larvae, encased in two triangular shells that are open on the oral side. Cyphonautes are planktotrophic larva that can eat and grow during their larval stage, allowing them to disperse much longer than the short-lived coronate and pseudocyphonautes larvae, both of which are lecithotrophic and do not feed in the plankton (Temkin and Zimmer 2002). Little is known about open ocean cyphonautes, including exactly how long they can last in the water column, which could vary significantly among species. Estimates for the larval duration of common cyphonautes range from 2 weeks to 2 months which provides the larva with ample time to cover vast distances in fast moving currents (Dudley 1973, Temkin and Zimmer2002).

Currents and larval distribution modeling

Cyphonautes are slow swimming larvae. They are considered a part of the plankton since they cannot swim fast enough to overcome ocean currents. However, cyphonautes have been known to swim or “crawl” upstream on the bottom where currents are slow, as a means of finding a favorable location for settlement (Abelson, 1997). Nevertheless, for most of their larval lives the effect of their swimming is negligible in comparison to the speed of the ocean currents in which they disperse.

Because of this, we can use ocean particle trajectory models to estimate the track that a cyphonautes larva may have taken during its larval life. An ocean particle trajectory model is a program that uses atmospheric and oceanic conditions and patterns to estimate the path that a particle will take during a certain timeframe. Current models typically use Lagrangian fluid

dynamics to model ocean currents and the effect they will have on objects floating on, or just below the surface. All of these models use datasets, often sourcing them from Universities such as Rutgers Universities Regional Ocean Modeling System (ROMS), or national science organizations like NASA's Estimating the Circulation and Climate of the Ocean consortium (ECCO). These trajectory models have a wide range of uses, from predicting where a capsized boat will end up, to backtracking to the origin of illegally smuggled drugs, to tracking larval distributions.

Over years of oceanographic cruises and larval sampling along the Western Atlantic Margin and the Gulf of Mexico, two main morphotypes of cyphonautes larva have been found. These will be referred to as morphotype 1 and morphotype 2 (Figure 1). I investigated the horizontal distribution, depth distribution and morphology to test the hypothesis that these two larval morphotypes represent two distinct species of Bryozoans that differ in vertical and horizontal distribution.

Materials and Methods

Study Sites and Larval Collection Methods

Between the years of 2011 and 2020, 6 oceanographic cruises occurred along the western margin of the Atlantic Ocean and around the Gulf of Mexico as part of two large studies conducted at the Oregon Institute of Marine Biology and sponsored by the National Science Foundation. Although these projects were focused on the larvae of deep-sea animals living at methane seeps, the plankton collections provided opportunities to analyze the distribution of many other species as well. These cruises collected cyphonautes, sometimes in large numbers, at 29 study sites, 15 along the western Atlantic margin, and 14 in the Gulf of Mexico.

During these cruises, larvae were sampled using two different kinds of equipment, a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) and the SyPRID Sampler. MOCNESS is the current standard for large-scale plankton collection. It is an improvement on the traditional sampling net because its opening and closing feature allows for sampling of discrete depths at a single site. The Environmental Sensing system provided specific details on depth and water properties so that the nets may be opened or closed at with the correct timing and the contents of the net may be examined with particular water conditions in mind (Wiebe et al. 1976). The SyPRID (Sentry Precision Robotic Impeller Driven) Sampler, affectionately nicknamed Plankzooka due to its resemblance to a Bazooka rocket launcher, is a larval sampler that gets mounted on a Sentry autonomous underwater vehicle (AUV). It uses spinning blades to gently pump water through the tubes and filter the microorganisms suspended in the water into a nylon mesh cod end. The SyPRID provides a way to maintain the structural integrity of delicate larva that would be damaged with more traditional larval collection methods

(Billings et al. 2016). OIMB scientists developed this modern sampler in collaboration with engineers at Woods Hole Oceanographic Institute and colleagues at Duke University.

Statistical Analysis

To compare depth distributions for the two morphotypes, I plotted the number of individuals of each morphotype that was found at each sampling depth. Percentages were used to better understand how each morphotype is spread out along the water column without the effect introduced by having a much greater abundance of morphotype 1. To determine whether the pattern of depth distribution was independent of morphotype, I ran a X^2 contingency assessment (test for independence) (Table 1). I subsequently calculated standardized residuals (Z scores)(Table 2) to determine whether the morphotype was found significantly more often in specific bins of the water column. This statistical analysis was run in R version 4.3.1.

To take a deeper look at horizontal distribution, abundance maps (Figures 3 and 4) were created in R, to demonstrate the study sites that collected the most individuals of each morphotype.

Trajectory Modeling

Reverse trajectory modeling was done using the trajectory modeling framework OpenDrift (v. 1.11.1). Within OpenDrift I used the specific simulation model OceanDrift. The oceanic and atmospheric data used in the framework was ECCO Ocean Velocity data collected from NASA's Earthdata database and run in Python. This combination has been shown to be effective through comparison to online dye tracking simulations and other ocean particle tracking software packages (Xiong and Macready, 2023). Imaginary particles (“larvae”) were seeded in varying numbers in at recorded coordinates for study sites where the cyphonautes were collected. A radius of about three kilometers was used with an even distribution throughout the radius to

get a better estimate of where the larvae might have come from and provide the potential for multiple diverging paths. Each reverse trajectory was run for two months to correspond to the longest larval duration. All simulations were run for surface currents and did not take vertical distribution of larvae into account.

Results

Morphology

Early on in image analysis it became apparent that there were two different morphotypes. These will be referred to as morphotype 1 and morphotype 2. The morphology of the two types of cyphonautes differ in a number of ways. Morphotype 1 has a much more angular shape, resembling a triangle, with the anterior end being convex and the posterior being concave. Morphotype 2 has a much more rounded shape (Figure 1), with both the anterior and posterior margins being convex. The two morphotypes also differ in size.

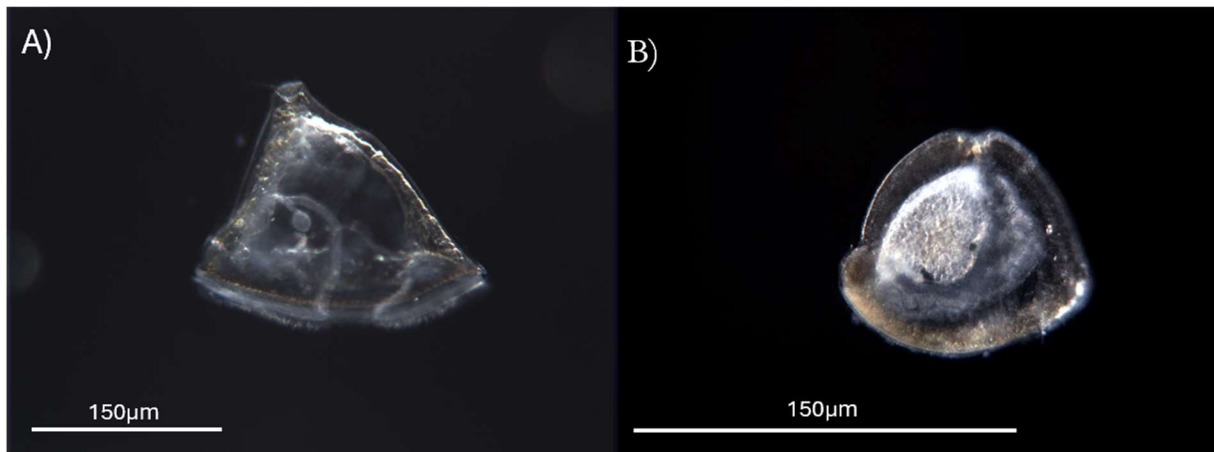


Figure 1: Cyphonautes Morphotypes.

A) Morphotype 1 B) Morphotype 2. Both photos were taken on an Olympus compound microscope with DIC optics.

The scale bars in figure 1 indicate a large difference in size between morphotype 1 and morphotype 2. Morphotype 1 is on average $406.8\mu\text{m}$ across the oral end with a standard deviation of $172.69\mu\text{m}$ and morphotype 2 is on average $65.6\mu\text{m}$ with a standard deviation of $14.82\mu\text{m}$. This represents a significant difference in size between morphotype 1 and morphotype 2.

Morphotype 1 was much more abundant than morphotype 2. Morphotype 1 had an average collection rate over all sites of 148.2 larvae per study site with a standard deviation of 356.9. Morphotype 2 had an average collection rate of 21.3 larva per site with a standard deviation of 39.0. The standard deviations for abundance were particularly large because there was a lot of variation in how many larvae were recovered between sites. There were sites where no cyphonautes larvae were recovered, and there were sites where thousands were recovered and this could be due to any number of factors, ranging from the geological conditions to the seasonality of bryozoan spawning.

Vertical Distribution

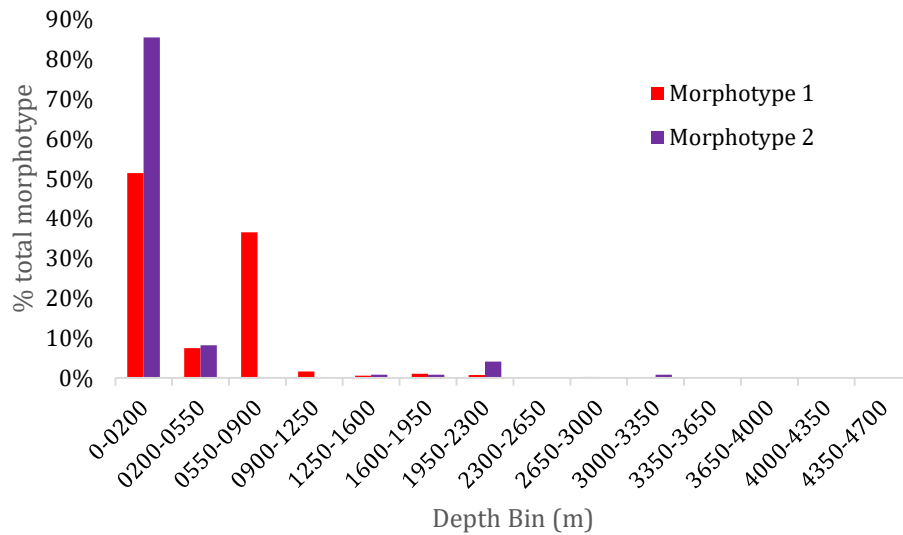


Figure 2: Vertical Distributions by morphotype

Colored bars represent the percentages of morphotypes present in each depth bin. Not all bins were sampled at every site because of depth differences among sites. Red corresponds with morphotype 1 distribution and purple corresponds with morphotype 2 distribution.

About 94% of all morphotype 2 cyphonautes were found between 0 and 200m deep, whereas only about 50% of morphotype 1 cyphonautes were found in the same depth bin. The majority of the remaining 50% of morphotype 1 were found between 550 and 900m. Morphotype 2 was

completely absent from this depth bin but was seen above and below this band. Morphotype 1 is visibly present as deep as 2300m, while morphotype 2 was visibly present as deep as 3350m (Figure 2).

Depth	0-200	200-550	550-900	900-1250	1250-1600	1600-1950	1950-2300	2300-2650	2650-3000	3000-3350	3350-3560	3650-4000	4000-4350	4350-4700
Morpho 1	0.021	0.455	0.003	0.281	0.449	0.456	0.063	0.429	0.416	0.226	0.468	0.445	0.445	0.445
Morpho 2	0.000	0.347	0.000	0.023	0.330	0.350	0.000	0.267	0.231	0.005	0.391	0.315	0.347	0.315

Table 1: P values of X² contingency assessment

Bolded cells highlight statistically significant P values (<0.05). Statistical significance indicates areas where the observed distribution deviated enough from the expected distribution if depth was independent of morphotype to not be due to random chance.

The X² contingency analysis, testing the independence of depth from morphotype showed significant interactions between the variables (X²_{13df}=196.91, p<<0.05) (Table 1). The large X² value shows that overall, there was a large difference between what we would have expected if morphotype had no impact on depth distribution versus the observed distributions, and the very low P value shows that the difference was enough that there was less than a 5% chance that such a large difference could have come from random chance. Standardized residuals (Table 2) show that the significant effects were driven by Morphotype 1 indicating an expected distribution in the surface layer but a stronger presence for the 550-900m range than would be expected if morphotype did not have an effect on depth distribution.

Depth	0-200	200-550	550-900	900-1250	1250-1600	1600-1950	1950-2300	2300-2650	2650-3000	3000-3350	3350-3560	3650-4000	4000-4350	4350-4700
Morpho 1	- 2.04	-0.11	2.76	0.58	-0.13	0.11	-1.53	0.18	0.21	-0.75	0.08	0.14	0.11	0.14
Morpho 2	7.04	0.39	- 9.55	-2.00	0.44	0.39	5.30	-0.62	-0.74	2.60	-0.28	-0.48	-0.39	-0.48

Table 2: Residuals table of X² contingency assessment

Bold values correspond with the statistically significant P values (table 1). Residuals demonstrate whether there was a positive or negative preference for a particular depth bin. A positive residual show that the morphotype was collected in that depth bin more than expected had the distributions been independent of morphotype. A negative residual shows that the morphotype was collected less in that depth bin than expected.

Morphotype 2 showed a stronger preference for the 0-200m and 1950-2300m ranges, while avoiding 550-900m and 900-1250m ranges more than expected.

Horizontal Distribution

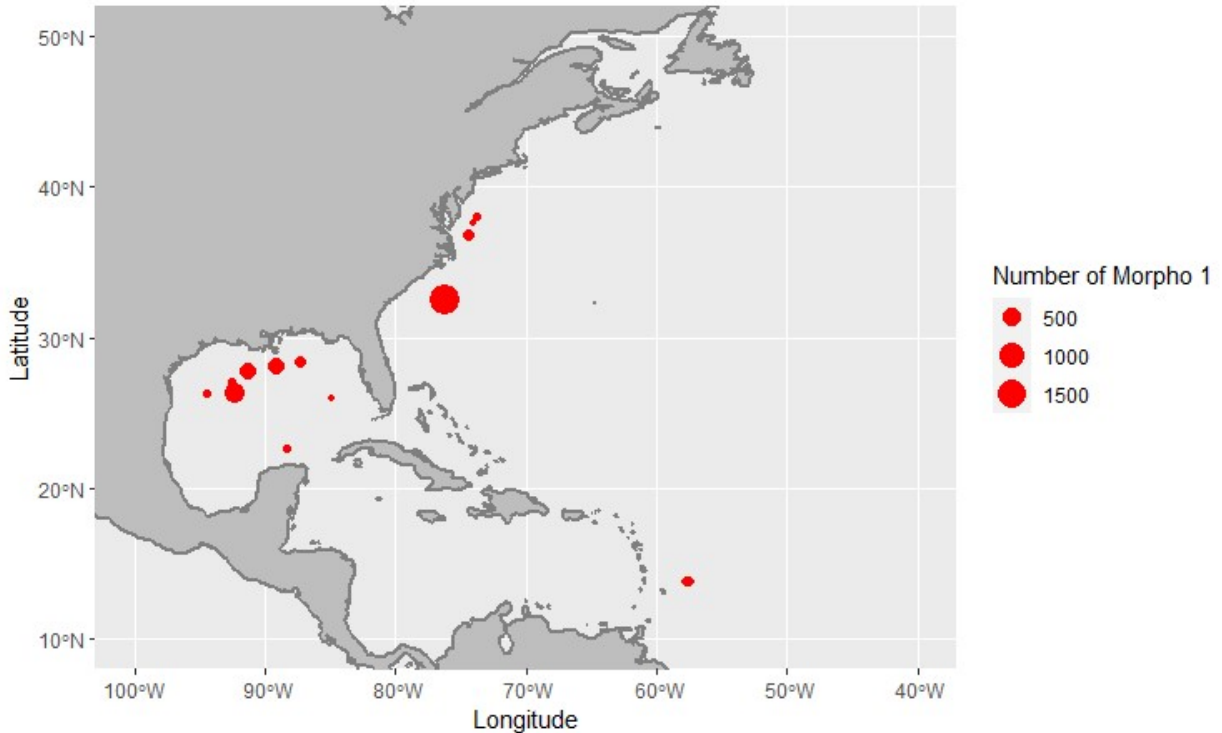


Figure 3: Morphotype 1 Distribution Map

Morphotype 1 is represented by red dots on the map. The size of the dots corresponds with the number of individuals found at those study sites.

The distribution map for morphotype 1 (Figure 3) shows that 42.8% of morphotype 1 was collected in the Gulf of Mexico, and 57.2% was collected along the western Atlantic margin.

Morphotype 2 shows a relatively consistent and widespread distribution, outside of the study site Norfolk Canyon which shows an unusually large abundance of morphotype 1 cyphonautes.

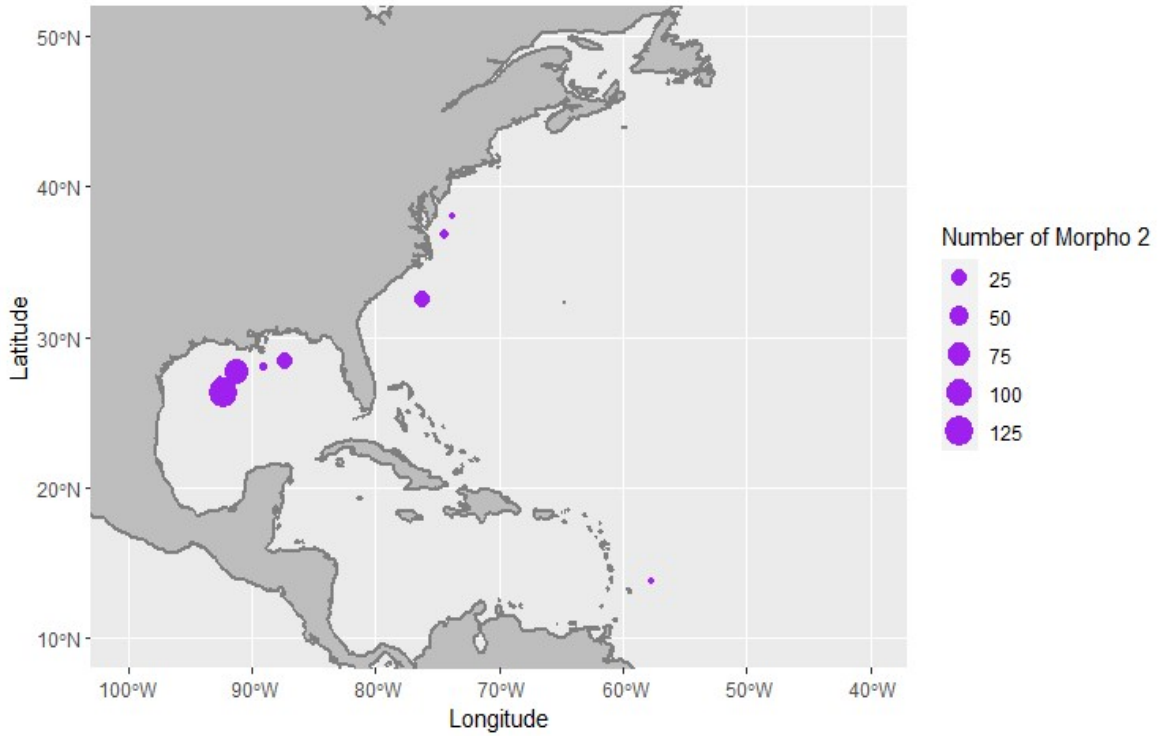


Figure 4: Morphotype 2 Distribution Map

Morphotype 2 is represented by purple dots on the map. The size of the dots corresponds with the number of individuals found at those study sites.

Figure 4 shows that 86.5% of morphotype 2 was found within the Gulf of Mexico, and 13.5% were collected on the western Atlantic margin. The majority of the morphotype 2 were collected within the boundaries of the Gulf of Mexico.

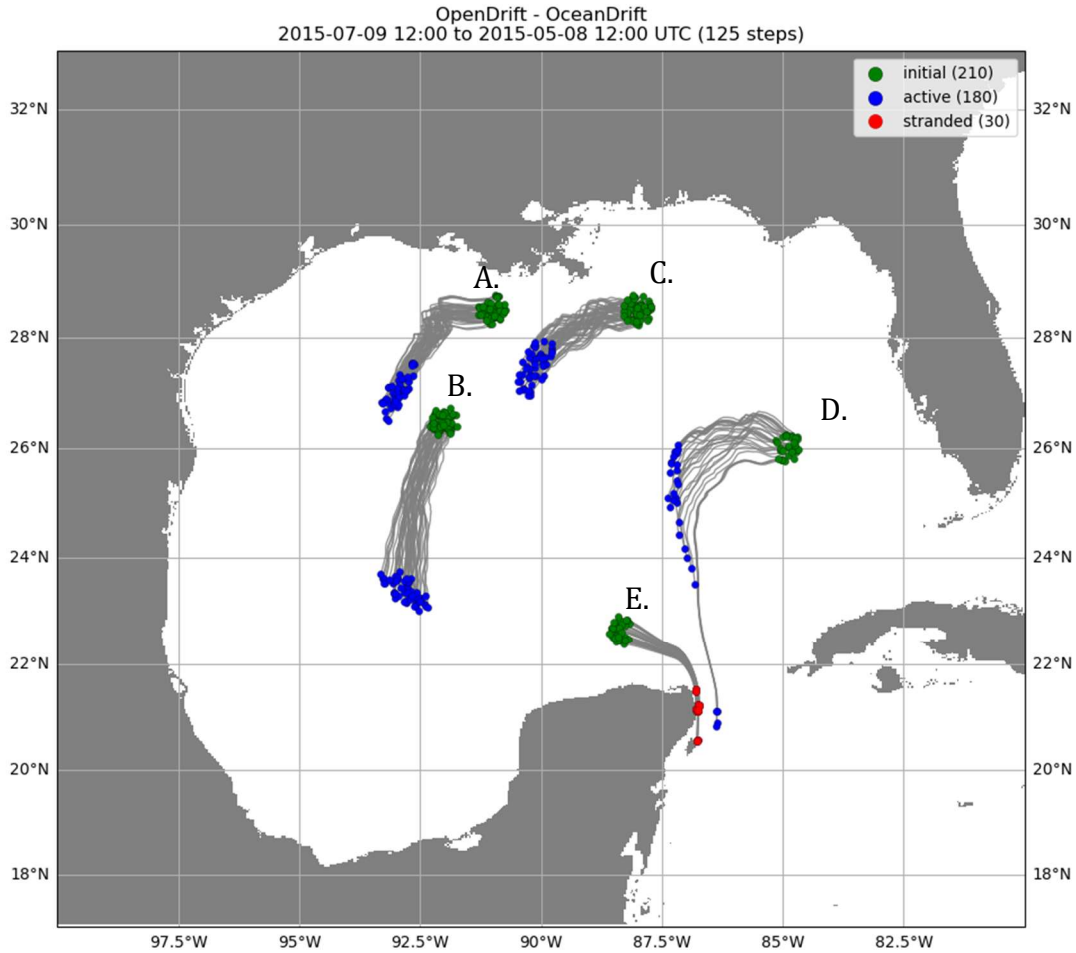


Figure 5: OpenDrift model of 5 study sites in the Gulf of Mexico

Shows the backwards trajectory of larva collected at different study sites within the Gulf of Mexico. A) site Brine Pool B) site AC645. C) site GB648 D) site Florida Escarpment E) site AT340. Green dots indicate the location the larvae were collected from, blue dots indicate potential location they could have come from based on ocean currents and wind patterns. Red dots indicate areas where the backwards trajectory collided with land.

Only sites AT340 and Norfolk Canyon, showed the backwards trajectory reaching land (Figures 5 and 6). Interestingly, at site AT340, only morphotype 1 was collected, and at Norfolk Canyon the vast majority of the cyphonautes collected were morphotype 1.

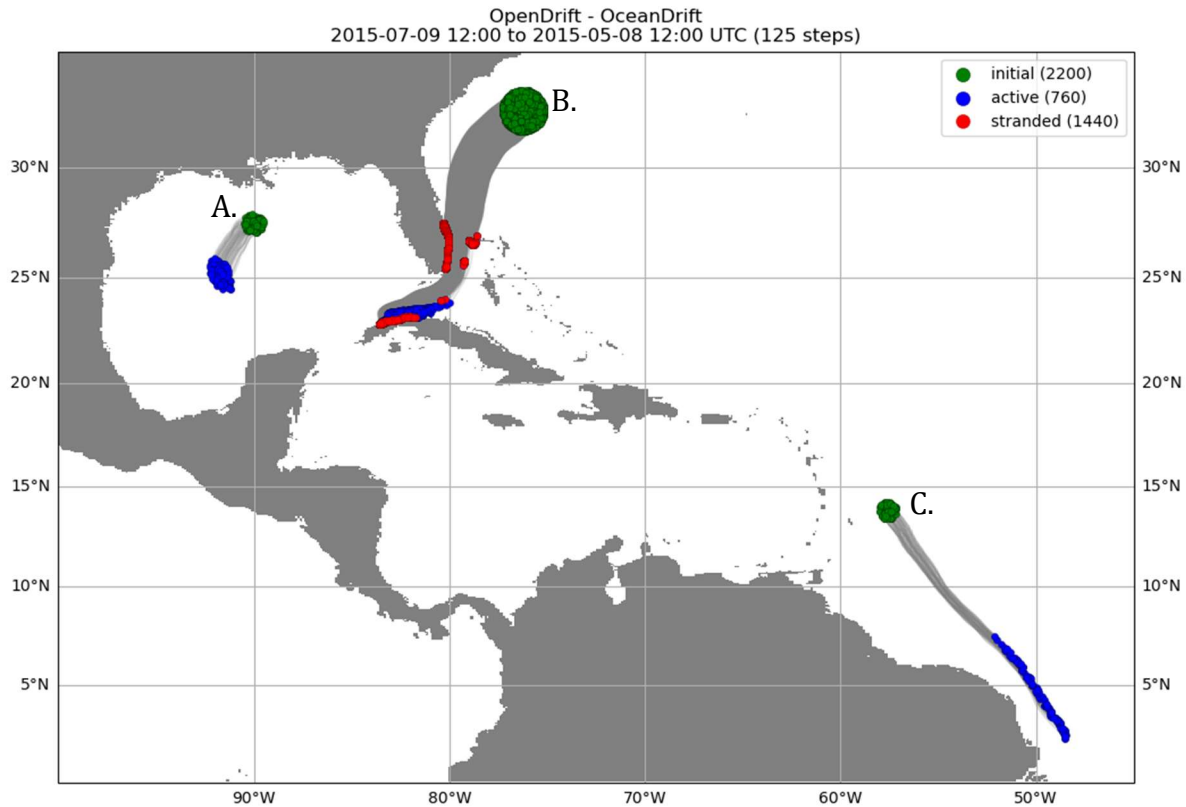


Figure 6: OpenDrift model of 3 study sites in the Gulf of Mexico and the Western Atlantic Margin Shows backwards trajectory of the larva collected at 3 different study sites, one within the Gulf of Mexico and two along the Western Atlantic Margin. A) site Bush Hill B) Norfolk Canyon C) Atlante. Trajectories were plotted over 2 months.

The backwards trajectory for the Norfolk Canyon study site (Figure 6 [B]) shows that the cyphonautes that were collected there likely originated from around Cuba or the southern tip of Florida and got caught in the gulf stream. It also shows that study site Atlante (Figure 6 [C]) collected larvae that likely came from off the coast of Brazil. The backwards trajectory for study site Bush Hill shows a much slower moving trajectory, one that originates in the middle of the Gulf of Mexico and only travels a bit North-East over two months.

Discussion

Species distinction evidence

Morphology has historically been the basis for species distinction and based on the large differences in size and morphology of morphotype 1 and morphotype 2, it is easy to conclude that they are different species.

Further, the vertical and horizontal distributions provide evidence that these two morphotypes experience very different life histories, even in their larval lives. Morphotype 1 is vastly more abundant than morphotype 2, which may indicate a morphotype 1 comes from a more abundant adult than morphotype 2, or that the adults of morphotype 1 produce more offspring than morphotype 1.

Further, the two morphotypes have different vertical and horizontal distributions, which provides more evidence that they are different species. The two morphotypes have different depth profiles, with morphotype 1 occupying a more vertically dispersed layer than morphotype 1 who shows up mainly within the top 200m (Figure 2). Also, their horizontal distributions are different from each other with morphotype 1 being relatively evenly spread throughout the Gulf of Mexico and the Western Atlantic Margin, where morphotype 2 is much more highly concentrated within the north of the Gulf of Mexico. The morphotypes occupy different spaces in the water column, both in terms of depth and in terms of geographic location. The two morphotypes having different distributions would imply that they have adapted to different conditions and survive within different ranges, something that is much less likely if they are the same species. In addition to the morphological and distribution evidence, genetic testing should be done in order to further verify this conclusion, as well as properly identify the species of these specimens.

Morphotype 1: Life history and origin

Working under the conclusion that morphotype 1 is a separate species from morphotype 2, we can postulate on the life histories and potential origins of the respective species.

Morphotype 1 larvae are likely produced by *Jellyella tuberculata* or a species with a similar life history. *Jellyella tuberculata* as an adult is a pseudoplanktonic bryozoan that commonly encrusts on the fronds of *Sargassum* weed and the shells of the planktonic gastropod *Janthina* (Taylor and Monks 1997). This pseudoplanktonic nature gives *J. tuberculata* a very large distribution, ranging from the southern tip of Africa to the Eastern Pacific Margin (WORMS, 2023). This widespread and mobile distribution of adult bryozoans would lead to a similarly widespread distribution of the *J. tuberculata* larva. If the adults of morphotype 1 have a similar life history to *J. tuberculata*, we would expect to see a relatively even distribution of the larva, with the exception of areas where multiple currents converge creating a dumping site for large amounts of drifting larva. For morphotype 1, we do see this relatively even spread, with the split being almost 50/50 for inside and outside of the Gulf of Mexico, with the exception of the study site at Norfolk Canyon (Figure 3). Norfolk Canyon is located right off the coast of the outer banks in North Carolina where the Mid-Atlantic Bight (MAB) shelf current is converging with the South Atlantic Bight (SAB) shelf current as well as the gulf stream. This convergence of currents catches larvae and creates a sink, which is likely why such a large number of cyphonautes were collected at this study site. Otherwise, we do see the even distribution we would expect.

The trajectory modeling shows that particular sites where only morphotype 1 was collected, such as Florida escarpment, AT340, and Atlante (Figure 5 [D, E], Figure 6 [C]), have backwards trajectories that suggest the larva came from the open ocean. We also see areas where study sites that mainly collected morphotype 1, such as AT340 and Norfolk Canyon (Figure 5

[E]and 6 [B]), have backward trajectories that suggest the larva would have come from the coast. The inconsistent coastal and open ocean origins could be explained by a pseudoplanktonic parent. If the adults are settled on a floating piece of *Sargassum*, then the adults may be washed into an intertidal coastline where they then reproduce and send out cyphonautes, or they may reproduce while in the open ocean. Particularly interesting is the combined backwards trajectory from Norfolk Canyon to the Florida Escarpment to Atlante. It shows the larva following the Atlantic Equatorial Currents, into the Gulf Loop current between the Yucatan peninsula and Cuba and then out of the Gulf of Mexico on the Gulf Stream. Having a strong distribution specifically along these three currents shows a particular adherence of these larva to the Atlantic's greater circulation system. This implies that these larvae are not coming from a coastal bryozoan, because these are very abundant in areas that they are being transported to by currents that are miles offshore. They are also not spawning at just one location and getting moved by these currents because cyphonautes have a larval duration lasting up to 2 months, so they are not going to be able to travel even half of their horizontal distribution in those two months as shown by Figure 6, indicating that there are adults all up and down these currents, and miles from the coast. This means that the bryozoans producing morphotype 1 cyphonautes are most likely either deep sea benthic bryozoans, or pseudoplanktonic bryozoans, drifting in the Atlantic ocean's current system.

To determine whether or not the parent bryozoans are benthic, deep-sea bryozoans or pseudoplanktonic bryozoans, we have to consider the vertical distribution of the larva. Morphotype 1 does have a relatively large vertical distribution, with the majority of the larvae being in the top 900m of water. If they were being produced by a benthic bryozoan, we would expect to have found more cyphonautes closer to the bottom where they were spawned than we

did find. Because the distribution tapered off so severely after 900m, we are led to believe that they are being spawned much closer to the surface, further supporting the hypothesis of a pseudoplanktonic lifestyle. It should be noted that the reverse trajectory models were only run over one time frame and that running the models during another time frame with different climate and ocean velocity data may show different trajectories. These models were run with the intention of seeing a general trend as opposed to particular locations. Future iterations of this study might include models run at multiple dates and a probability of origin map showing the areas that most commonly were the ending point of the reverse trajectory to account for error introduced by the model.

Morphotype 2: life history and origin

Morphotype 2 larvae are likely produced by a coastal bryozoan that spawns from inside the Gulf of Mexico. This is supported by the horizontal distribution being mainly within the northern Gulf of Mexico as seen in Figure 3. Morphotype 2 was rarely found outside the Gulf of Mexico. The locations along the western Atlantic margin where morphotype 2 was collected were areas along the gulf stream, and the number of morphotype 2 cyphonautes collected got smaller further from the gulf (Figure 3). There was one exception to this, and that is the one morphotype 2 cyphonautes found near Barbados at the Atlante site. This could be due to an error in morphotyping, or unusual circumstances such as the larva being caught in ballast water in ships from the Gulf of Mexico (Dulière and Guillaumot et al, 2022). It could also be that morphotype 2 is present around Barbados, and if this is the case, it would contradict the hypothesis that morphotype 2 originates from the Gulf of Mexico, because there are not many natural ways for a weakly swimming larva get out of the Gulf of Mexico and travel south against the North Atlantic Equatorial Current.

The trajectory modeling for the sites where morphotype 2 were mainly collected from, such as Brine Pool, AC645 and GB648 (Figure 5, [A, B, C]), showed that within the 2 months that the simulation ran, the cyphonautes didn't move very much. According to the model these cyphonautes were spawned from bryozoans toward the center of the Gulf of Mexico. This could support a hypothesis that morphotype 2 spawns from a deep-sea benthic bryozoan in the Gulf of Mexico. The main contradiction would be vertical distribution. 90% of morphotype 2 cyphonautes were found in the top 200m of water (Figure 2). It is possible to consider that because a higher percentage of morphotype 2 was found at deeper depths that maybe they are being spawned in the deep then quickly floating towards the surface, however if that were the case I would still expect to see greater numbers of morphotype 2 at the depths they are being spawned at. Another explanation could be that morphotype 2 were being spawned on the coasts in large numbers and the ones that were collected were the relatively rare individuals that got swept away from the coast in a series of Gulf eddies. This is supported by the much lower abundance of morphotype 2 that was seen in comparison to morphotype 1 as well as the vertical distribution being highly concentrated towards the surface layer.

In conclusion, there are fewer data suggesting the particular life history of morphotype 2, but there is substantial evidence suggesting that morphotype 2 is being spawned by a bryozoan inside of the Gulf of Mexico.

To continue this investigation into these two morphotypes, genetic analysis would be invaluable in determining the identity of the adult bryozoans, which will then reveal more about the life history of these larva. It would also be interesting to continue with the trajectory modelling, make more specialized models, including depth movement, more specific particle characteristics, and additional timeframes that would match the specific collection dates.

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