



Two-year survey of *Alitta succinea* (Annelida: Nereididae) in fouling communities with notes on morphology and reproduction

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ABSTRACT

Alitta succinea (Leuckart, 1847) is an errant segmented worm from the Nereididae family (Annelida) and is broadly distributed around the greater Atlantic basin. *A. succinea* is a resilient mobile omnivore that plays an important role in connecting lower and upper levels of the food web. Like many other nereidids, *A. succinea* metamorphoses into reproductive swimming forms, called epitokes, before entering the water column to spawn. In Galveston, Texas the species *A. succinea* is commonly found in fouling communities attached to artificial structures in marinas. This study presents a two-year survey of a population found in the Texas A&M University at Galveston Boat Basin. Over the two-year period, we collected over 2,000 *A. succinea* individuals for a gross comparison of population dynamics and morphometrics. During the summer, we found high numbers of small individuals, indicating a primary recruitment period. This was further corroborated by the high number of epitokes in the summer compared to the winter and spring. During the summer and fall, the observed epitokes were significantly smaller than those found in the winter and spring, which supports previous research that shows a positive relationship between temperature and developmental rates. The continual presence of epitokes indicates the existence of a recruitment process that occurs continuously throughout the year. In terms of morphometrics, atokes and epitokes, both females and males, had their own unique profiles. As we expected, epitokes have larger eyes and wider posterior segments compared to atokes. Interestingly, we found females to be significantly larger than males, no matter the season. This study presents an updated approach to staging sexually reproductive individuals to help standardize taxonomic descriptions.

Keywords: Epitoky, Morphometrics, Metamorphosis, pileworm, Population Dynamics

INTRODUCTION

Fouling communities, considered a nuisance by some, are assemblages of living organisms, attached to submerged structures and composed

of diverse flora and fauna (Scheer, 1945). These assemblages contribute to bottom-up energy transfer to inhabitants of the adjacent water column and experience seasonal population fluctuations, made evident by algae growth rates and ebbs and flows of community composition (Detwiler et al., 2002). Commonly represented animal phyla are Chordata (Ascidiaeaceae), Arthropoda (Crustacea, Chelicerata), Annelida (polychaetes), Mollusca (Bivalvia, Gastropoda), Platyhelminthes (Acotylea), Nemertea, Bryozoa,

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Cnidaria (Hydrozoa), and Porifera. Since they often grow on artificial substrates in ports and boat basins, fouling communities are frequently home to introduced and invasive species released from ballast water, which increases the importance of monitoring these assemblages (Cariton and Geller, 1993; Ruiz et al., 2000). These habitats experience a variety of stressors, both seasonal and punctuated. Animals living within these environments must be resilient to changes in abiotic factors including temperature, salinity, and dissolved oxygen (Khalaman, 2013; Fernández-Romero et al., 2019).

Some of the errant polychaetes found more commonly within fouling communities and soft bottoms in Southeast Texas are the nereidid worms, *Alitta succinea* (Leuckart, 1847) (Figure 1A) (Calnan et al., 1979). They live at the interface of sediment and water, both in shallow 'U'-shaped burrows, sometimes lined with mucus, and on the benthos, as epifauna (Gillet et al., 2011; Aguiar and Gomes Santos, 2018). *A. succinea* can survive in euryhaline and eurythermal environmental conditions and have a strong tolerance for changes in oxygen saturation, including hypoxic conditions

(Kersey-Sturdivant et al., 2015). They have been found in temperate and tropical estuaries (Zeeck et al., 1990; Sette et al., 2013), brackish waters of the Baltic Sea (Rasmussen, 1973), and in the potassium chloride rich waters of the Salton Sea (Carpelan and Linsley, 1961). Typically, they feed on detritus, algae, and small crustaceans. *A. succinea* populations likely play an important role in community composition, as predatory omnivores and as prey to higher trophic-level grazing predators (Gillet et al., 2011).

A. succinea populations are successful in a variety of climates and ecosystems worldwide. However, when considering population dynamics, compositions can be driven by fluctuating local environmental factors. In the tropics, where temperature is stable throughout the year, *A. succinea* reproduce continually, producing new cohorts throughout the year (Sette et al., 2013). In a temperate climate, two annual population peaks occur, indicating two seasonal reproductive events (Gillet et al., 2011). In general, temperature has been found to drive reproductive development, while other factors (i.e. the lunar cycle) drive reproductive events (Fong, 1991).

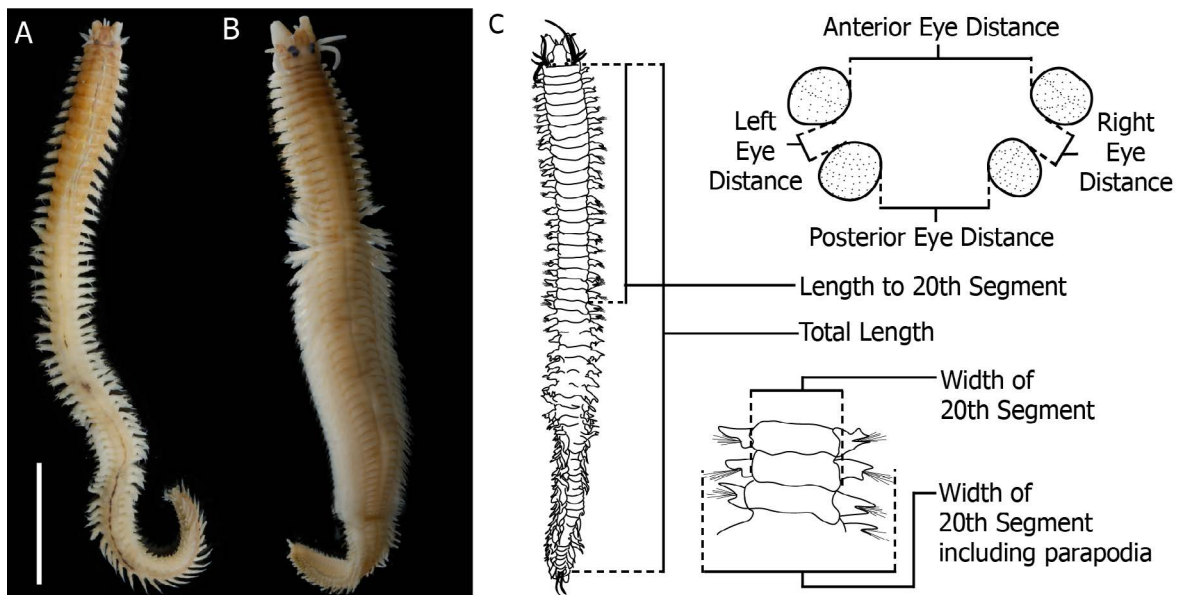


Figure 1. *Alitta succinea* A) Atoke, or benthic morph with small eyes and uniform parapodia. B) Male epitoke with hypertrophied eyes and modifications in parapodia occurring on the 15th segment. (Scale bar = 5cm for both A and B) C) Schematic drawing of an atoke with its morphometrics. Speckling in the eyes denotes the surface area measured for each eye.

Alitta succinea present epitoky, meaning they undergo a sexual metamorphosis before reproducing. The benthic worm (atoke) undergoes an incomplete metamorphosis, then, upon specific cues, moves into the water column to spawn (epitoke) (Clark, 1961; Figure 1B). Externally, the morphological differences between the atoke and epitoke are most egregious in the eyes and posterior segments (referred to as the modified zone). The modified zone typically starts at chaetiger 15 in males, and between chaetiger 16-17 in females (Villalobos-Guerrero and Carrera-Parra, 2015). In the modified zone, the parapodia change from small, blunt lobes with fine chaetae, adapted to move through sediment, to enlarged flattened lobes with wide, paddle-like chaetae, better suited for swimming. Both pairs of eyes then experience hypertrophy. Although the exact anatomical mechanics of eye transmutations in *A. succinea* have not been documented, the ultrastructure of a closely related species, *Perinereis brevicirris* (Grube, 1847), has been compared in atoke and epitoke stages, showing a 10-fold increase in the width of the inner rhabdomic layer (Miyako-Shimazaki et al., 2005). This increase in size is the result of an extension of their photoreceptor processes through photoreceptor membrane synthesis (Miyako-Shimazaki et al., 2005).

Internally, the gut of *A. succinea* atrophies, allowing for the vacant coelomic cavity to fill with gametes. Musculature also changes depending on the body region: it atrophies in the anterior unmodified zone and hypertrophies in the modified zone (Clark, 1961). Behaviorally, the worms forgo foraging and center all their energy on morphological transmutation and gamete development before swarming. This process is induced by a combination of pheromonal cues, temperature fluctuations, and lunar phases, and causes reproductive individuals to leave the benthos and enter the water column in a 'nuptial dance' (Lillie and Just, 1913; Hardege et al., 1990). This dance is orchestrated by a pheromone trail released by the females, which males respond to (Ram et al., 2008). Males are then guided by a peptide cue to follow the females (Ram et al., 1999). A pheromone exchange occurs, triggering the release of a plume of gametes by the males, then by the females (Bartels-Hardege and Zeek,

1990; Ram and Hardege, 2005; Ram et al., 2008). After gametes are expelled, individuals expire from metabolic exhaustion or from ruptured body walls due to gamete expulsion (Ram and Hardege, 2005; Aguiar and Gomes Santos, 2018). Then, the dead worms either sink to the sediment or are consumed by prey, contributing to an influx of organic material into the environment either way (Ram and Hardege, 2005).

It is important to consider reproductive events and population dynamics for species management (especially in invasive species, or fouling community removal), trophic-level interaction studies, and general biodiversity surveys. Long-term monitoring projects with frequent sampling, such as the one presented here, can help elucidate local patterns and explain broader biological processes. This project aims to shed light on the population dynamics of the epitokous nereidid *A. succinea* throughout an annual seasonal cycle in a sub-tropical temperate environment. We anticipate that, similar to what happens when populations experience seasonal temperature variation, there will be two population peaks indicated by high numbers of small worms during the late spring and early fall (Gillet et al., 2011; Aguiar and Gomes Santos, 2018). These peaks will be preceded by an increase in late-stage epitokes during the early spring and late summer. In addition to describing the population, this project aims to collect detailed morphometrics of individuals to better understand the juvenile to adult (atoke) to sexually mature (epitoke) ontogeny.

METHODS

STUDY AREA

Sampling efforts were conducted at the Texas A&M University, Galveston Small Boat Basin, from January 2020 to December 2021 (Figure 2). This boat basin has restricted boat traffic and is primarily used to dock the university's teaching and research vessels. It has an opening to the Galveston Shipping Channel, which flows into Galveston Bay and connects to the Gulf of Mexico from there. Galveston, Texas has seasonal temperature variations, with hotter (average air temperature: 32.4°C) summers

(July-September), mild springs (April, May, June) and falls (October, November, December), and colder (Average air temperature: 19.9°C) winters (January-March) (NOAA, Climate Graphs). In 2020 and 2021, the temperature dropped below freezing point for three days in February 2021, during an isolated freeze event. The air temperature is reflected by the seasonal water parameters, with the highest temperatures in the summer and the lowest ones in the winter (Table 1). Water parameter data from the boat basin was collected by the Texas Conversation Action Place through the State Wildlife Grant (Texas Parks & Wildlife Department #802, TPWD Contract No. 528672). Observations were made with a MS5

Hydrolab water quality sonde daily or as often as possible according to personnel availability and safety conditions.

The boat basin has a series of floating finger-docks with one main axis and five offshoot piers. The docks are composed of black polyvinyl floats that and rise and descend along with the diurnal tide, always remaining partially submerged. The floats are covered year-round with fouling communities that are not disturbed by any kind of maintenance. Each float has an exposed face measuring 30x100cm, of which a 15x100cm area was fouled. Each float was assigned a number and a random number list was generated to determine the sampling order.

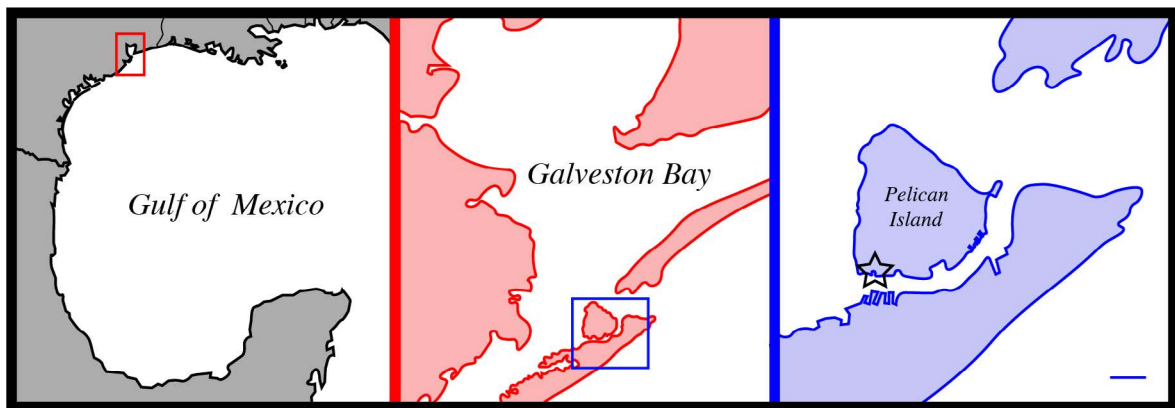


Figure 2. Field site located in the Northern Gulf of Mexico along the Southeast Texas Coast. Star indicates field site on Pelican Island. The scale bar for the blue map is 1 kilometer.

Table 1. Mean water parameters for study site grouped by season. Values presented for 2020, 2021. Significant difference between years noted with an asterisk. Minimum and maximum values are from combined years.

Season	Temperature (°C)	Salinity (ppt)	DO (mg/L)	Observations
Winter	15.85, 14.3*	23.21, 23.92	8.42, 8.66	70, 59
Spring	24.2, 22.9	16.34, 18.42	6.9, 7.12	40, 79
Summer	29.8, 29.98	25.43, 21.03*	5.59, 5.78	48, 49
Fall	22.45, 22.69	24.64, 24.04	6.8, 6.8	79, 55
Min, Max	9.91, 27.1	7.62, 32.6	3.81, 11.3	40, 79

SAMPLING DESIGN AND COLLECTION

On the second Monday of every month from January 2020 to December 2021, sampling efforts were conducted. In September of 2021, Tropical Storm Nicholas created unsafe conditions for the conduction of study, which resulted in the collection being postponed for two days. Fouling communities were entirely scraped off the floats with a pallet knife and all material was collected using a dip net. Contents were placed in a tub with ambient sea water and immediately taken to the lab for sorting. All worms were extracted from the scrapings using forceps, which allowed researchers to tease through the algal mats first with the naked eye, then using a Leica S8AP0 stereoscope. Individuals were identified as *Alitta succinea* based on recent descriptions by Villalobos-Guerrero and Carrera-Parra (2015). The identification was verified in four specimens by means of a DNA barcoding approach (see [Supplementary Material](#)). After extraction and identification, all individuals were placed in 7% Magnesium Chloride for 5-10 minutes. Thereafter, collections were moved to 4% formalin for 36-48 hours, then transferred to 70% ethanol for long-term storage.

MORPHOLOGICAL DOCUMENTATION

Worms were individually measured with calipers (0.01 mm) and a stereoscope. For each individual, measurements of total length, length to the 20th chaetiger, and width of the 20th chaetiger including and excluding parapodia were recorded (Figure 1C). Only complete specimens, identified according to the presence of the pygidium, were measured for total length. Both the total length and length to the 20th chaetiger measurements started at (and included) the tentacular belt, previously regarded as the peristomium, as pharyngeal expulsion often changed the position of the prostomium (Villalobos-Guerrero et al., 2021). The width of the chaetiger was measured to and from the base of the parapodial attachment at the body wall. To better understand the distribution and variation of atoke's sizes within seasons, we created size classes based on the average length to the 20th chaetiger of all collected atokes. Size class 1

included the smallest worms, with the length to the 20th chaetiger of individuals from the lowest quartile, while size class 4 had individuals from the largest quartile. The width including the parapodia was measured from tip to tip of the extended chaetae. For weight measurements, individuals were removed from the ethanol and blotted on tissue paper for two seconds. They were then measured on a Denver Instruments analytical balance to the nearest 0.0001 gram. Only complete individuals were weighed: the scale could not weigh individuals measuring less than 5 mm, so they were assigned a weight of 0.0.

The prostomium of all individual worms were imaged using the same stereoscope, outfitted with a Canon DSLRebel500. Images were processed for eye morphometrics on the open-source software ImageJ using the area and measure functions (0.000000001) (Figure 1C). For each image, the measurements of the following areas were recorded: anterior left eye (ALE), anterior right eye (ARE), posterior left eye (PLE), and posterior right eye (PRE). The total eye area was calculated summing all measurements. The shortest distance between ALE and ARE was measured as the distance between anterior eyes. This method was replicated to measure the distance between posterior eyes (PLE to PRE). These two values were averaged to find the average distance between anterior eyes and posterior eyes. The measurement from the ALE to the PLE was found to be the distance between left eyes, and the same occurred for the measurement from the ARE to the PRE. These were then averaged to calculate the distance between left eyes and right eyes.

All individuals were assessed for signs of epitoky and staged with the system outlined by Aguiar and Gomes Santos (2018) with minor modifications. In short, Stage I epitokes were identified by their thickened middle or posterior regions, which are this way because of the developing oocytes or sperm. After weights were assessed, a small incision in a posterior segment was made to release individuals' gametes and determine their sex. Females in Stage II did not

present any external modifications, however, oocytes plaques were spread throughout their bodies and their mid to posterior section was wider than the anterior section. For Stage II males, the dorsal and/or ventral cirri were beginning to show signs of serration. Stage III females and males presented parapodial modifications, a distinct boundary between the anterior unmodified zone and the posterior modified zone, and enlarged eyes. Males' dorsal and ventral cirri had well developed serration. For both sexes, Stage IV was defined by the presence of exposed natatory chaetae. For individuals in Stage III or IV, the first modified chaetiger number was recorded.

DATA ANALYSIS

Data visualization and statistical analysis were conducted in R (R version 4.2.2) and RStudio version 2022.12.0 programs. To focus on the seasonal comparison, months were pooled into seasons based on temperature relative to each time of year. When comparing environmental parameters and morphometrics or counting data between years by seasons or between sexes at the same stage, Welch's t-test was used to determine significance. A linear regression model was run to find the best (highest adj. R^2) correlation between total length and other measurements. The Kruskal-Wallis test was used to compare seasons, and Dunn's test was used for the post-hoc analysis. To compare stages, an ANOVA was run with Tukey's HSD post hoc test. If $p > 0.05$, values were considered significant.

RESULTS

ENVIRONMENTAL PARAMETERS

Over the two-year survey, environmental parameters such as temperature, salinity, and DO were recorded on 479 out of 730 days. Temperatures in 2020 and 2021 did not significantly differ during the different years' springs, summers, and falls. The winter of 2021 was significantly colder than that of 2020 ($p < .005$), however, the months were still pooled

for the overall trend comparison, as both winters were significantly colder than any other season (Figure 3A). The spring of 2021 and both falls did not differ significantly in temperature. The spring of 2020 was significantly warmer than the fall of the same year, although only slightly significantly ($p = 0.028$)

During the winter, spring, and fall, salinity did not significantly differ between years. The summer of 2021 had a significantly lower salinity than that of 2020, likely due to the Tropical Storm Nicholas. During the spring, salinity was lower than in all other seasons. Winter, summer, and fall had similar salinity rates, although during the winter salinity levels were slightly lower than in the fall ($p = 0.04$) DO levels did not significantly vary between the seasons of different years, however, the winter did present a significantly higher DO rate while the summer had a significantly lower one. Spring and fall had similar DO levels. Both summers were significantly warmer than all other seasons.

POPULATION DYNAMICS

In total, 2,164 worms were collected from fouling communities during the two-year survey. In 2020, collections ranged from a high of 117 individuals in October to a low of 18 in March. In 2021, they ranged from 211 in August to 20 again in March (Figure 3B). When grouped by season, it can be noticed that both years followed the same trend, with population rates peaking in the summer and declining through the fall, winter, and spring (Figure 3C).

Sixty-six epitokes were collected, with an overall M:F sex ratio of 1:1.06. The females were collected evenly between 2020 and 2021, with 17 individuals found each year. Twenty-five males were collected in 2020 and the remaining 7 in 2021. Two thirds of all epitokes were collected during the summer and fall (Figure 3D). Females were most often collected in Stages I (9), II (13) or IV (11), and only one Stage III female was identified. Males's distribution was relatively even through Stages I-III (5,6,5), however, 15 Stage IV males were collected. No epitoke stages were found to predominate on specific seasons.

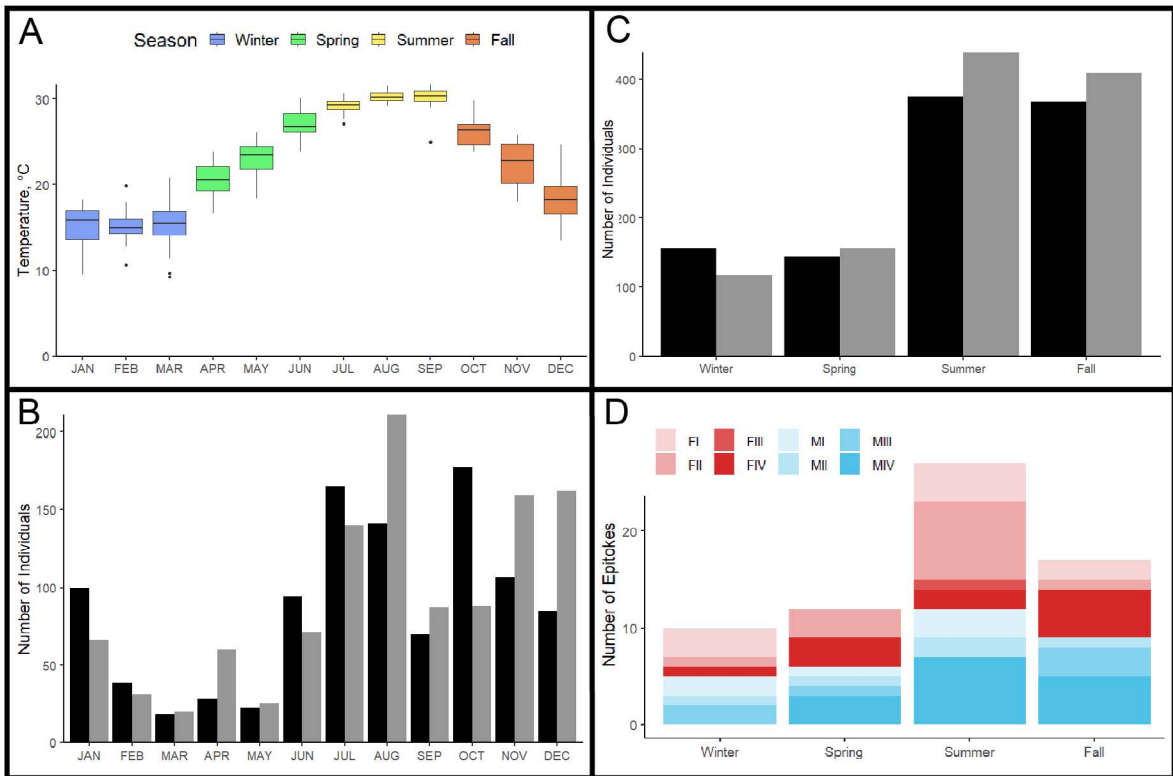


Figure 3: *Alitta succinea* population variations throughout seasons, present both in numbers of atokes and of epitokes. A) Water temperature variation over the two-year survey time period, months of 2020 and 2021 batched to show trends. B) Total number of individuals collected by month and C) by season. Black bars indicate the samples collected in 2020 and grey bars indicate those collected in 2021. D) Number of epitokes by season according to their stages.

MORPHOMETRICS

A total of 13 measurements were collected from each fully intact individuals, which resulted in a potential morphometric analysis of 28,132 observations. The “largest” worm, (total length*wet weight) was collected in February of 2020 and was a female epitoke measuring 47.08 mm and weighing 0.22 g. The smallest worm had a total length of 1.05 mm (10 total segments) and was collected in August of 2021.

In total, 70% (1,505) of all collected worms were fully intact. Of the remaining 30%, 428 had at least the first 20 chaetigers intact. Measurements of total length and length to the 20th chaetiger has the strongest correlation ($R^{2adj}=0.89$) out of all measurements taken. By using the length to the

20th chaetiger measurement as a proxy for total length, our effective sample size, composed of fully intact worms, increased to 1,933, that is, from 70% to 89% of all collected worms.

Comparison of the seasons between years showed significant differences in all measurements excluding wet weight of Winter and Spring (Table 2). However, seasonal data were pooled, since when analyzed visually, the years did exhibit similar trends. Among seasons, the fall and summer had their own significantly unique morphometric profiles. Spring and Winter had similar lengths to the 20th chaetiger, width of the 20th chaetiger including parapodia, and wet weight, but did have significantly different widths of the 20th chaetiger. The smallest atokes were found in the summer and fall (Table 2).

Table 2. Average collections and morphometrics for all individuals collected by Season. Averages listed for 2020, 2021. Significant differences between years are noted with an asterisk.

Season	Total Collected	Epitokes Collected (F:M)	Length to the 20 th (mm)	Width of 20 th (mm)	Width of 20 th , Including parapodia (mm)	Wet Weight (g)
Winter	156, 117	1:5, 4:0	6.92, 5.72*	1.16, 0.86*	2.1, 1.61*	0.0314, 0.0268
Spring	144, 156	5:5, 1:1	6.46, 5.78*	0.98, 0.79*	1.88, 1.52*	0.0179, 0.0144
Summer	375, 438	10:9, 5:3	4.93, 4.61*	0.79, 0.62	1.54, 1.22*	0.0092, 0.0068*
Fall	368, 409	1:6, 7:3	3.95, 4.7*	0.56, 0.68*	1.06, 1.31*	0.0075, 0.0114*
Annual	1,044, 1,120	17:25, 17:7	5.12, 4.94	0.8, 0.7	1.5, 1.34	0.014, 0.012

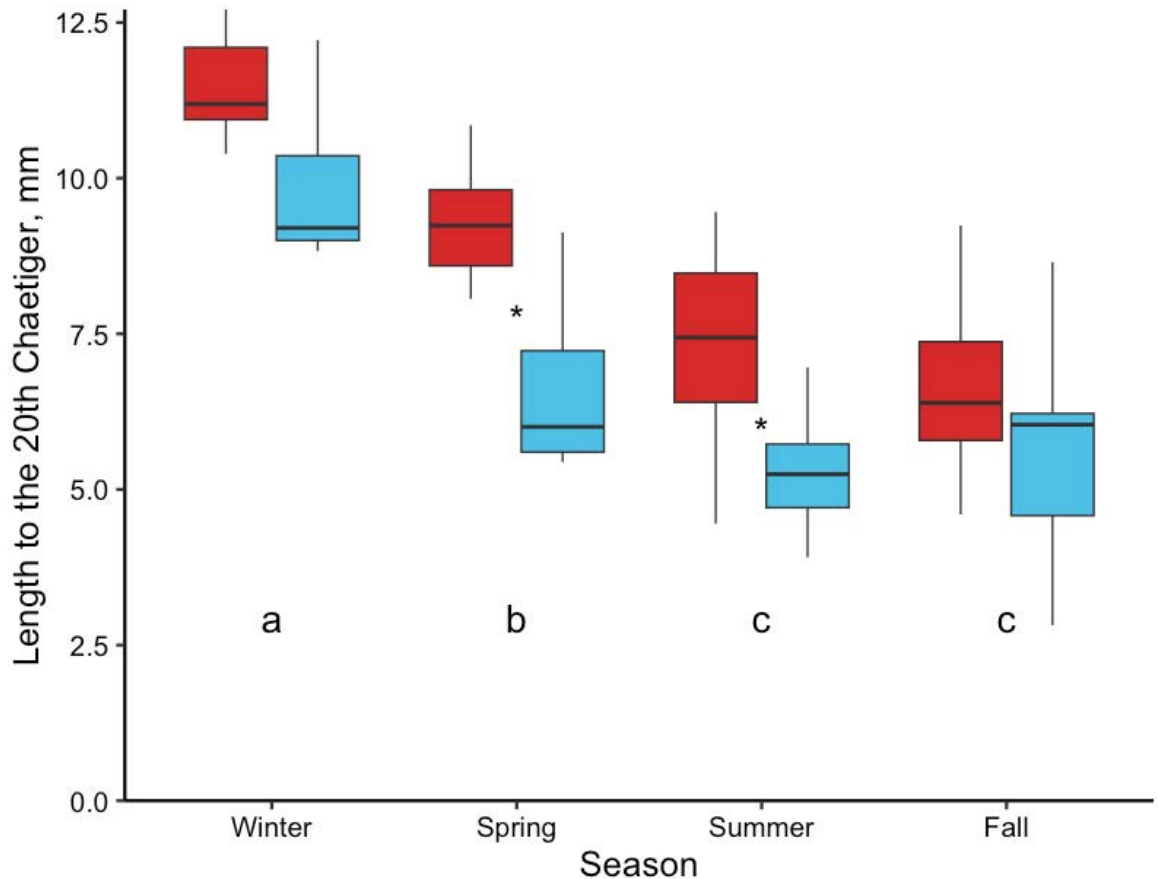


Figure 4. Variations of the length to the 20th chaetiger of all epitokes across different seasons. Red boxes indicate females, blue boxes indicate males. The epitokes found in the winter were significantly longer than in any other season. In the spring, we found larger epitokes than in the summer and fall. The asterisks indicate a significant difference between the length of different sexes within that season.

Table 3. Average morphometrics of all individuals collected in different reproductive stages. Minimum, maximum values reported under each average. The asterisks indicate significant differences between females and males.

	Female	Male	Atoke
Total Collected	34	32	2,098
Length to the 20th segment, mm	8.10*	6.33	4.95
	4.45, 12.7	2.82, 12.2	1.78, 14.4
Width of 20th segment, mm	1.66*	1.33	.72
	1.02, 2.52	0.5, 2.57	0.11, 2.53
Width of 20th segment including parapodia, mm	3.1*	2.65	1.38
	1.85, 5.18	1.46, 4.69	0.29, 4.49
Wet Weight, g	0.064	0.041	0.011
	0.009, 0.223	0.007, 0.162	-, 0.175
Total eye area, mm²	0.099	0.093	0.016
	0.023, 0.199	0.037, 0.174	0.001, 0.169
Average distance between anterior eyes and posterior eyes, mm	0.556*	0.454	0.315
	0.341, 0.875	0.262, 0.864	0.084, 0.793
Average distance between left eyes and right eyes, mm	0.037*	0.022	0.039
	0, 0.078	0, 0.083	0.004, 0.221

The average length to the 20th chaetiger was 5.028 mm for all atokes. Size class 1 contained individuals with a length to the 20th measuring less than 3.65 mm. For size class 2, this measure was greater than that of size class 1, but lower than 5.028 mm. This pattern continued for size class 3, which had a measure lower than 6.87 mm and greater than that of size class 2, and for size class 4, which had a greater measure than size class 2 and

included the largest length: 14.44 mm. We found few size class 1 individuals during the winter and spring, and greater numbers of these individuals in the summer and fall. Size class 2 followed the same pattern, while numbers of size class 4 individuals remained stable throughout the year.

As expected, atokes and epitokes had significantly different morphometric profiles (Table 3). In all morphometric measurements,

epitokes were found to be longer, wider, and have larger eyes that were closer together than those of atokes. Most female epitokes were significantly longer and wider than males, however, wet weight values did not significantly differ between sexes. When observing length differences between sexes across seasons, we found that females were only significantly larger than males during the spring and summer (Figure 4). Overall, epitokes were significantly longer in the winter than in any other season, but they were also significantly longer in the spring than in the summer and fall (during which epitoke's measures did not significantly differ) (Figure 4). The first modified chaetiger in females ranged from number 17 (7), 18 (3), and 19 (2). The two females with modifications starting on chaetiger 19 were in Stages III and IV. They could still be developing structures on chaetigers 17 and 18, although no external features indicated this. For 19 out of the 21 males collected, the first modified chaetiger was number 15. For the two remaining males, the modifications started on chaetiger 16, however, both individuals were in Stage III and could still be developing structures on chaetiger 15.

The stages of epitokes of different sexes did not strongly influence their morphometrics. For males in Stage I, the length to the 20th chaetiger was significantly longer than for those in Stage IV. Additionally, the eyes of males in Stage IV were closer together in both the A-P axis and L-R axis.

DISCUSSION

Alitta succinea populations found in fouling communities from Southeast Texas coast go through an annual population cycle, peaking in the warm summer and in the fall, with the presence of small individuals. Although in smaller numbers than atokes, epitokes occur in the population all year round, and the majority of them can be found in the summer and fall. This pattern indicates that the primary spawning season occurs during the months that coincide with the highest temperatures and a smaller amount of continuous background spawning occurs throughout the year. Morphologically,

epitokes are longer and wider than atokes, and females tend to be larger than males. Furthermore, we were easily able to apply the staging system proposed by Aguiar and Gomes-Santos (2018) to a population from a different geographic region, which reaffirms the utility of presenting observations under this staging system.

POPULATION DYNAMICS

The population dynamics we observed seem to follow a pattern that is similar to one described in a tropical lagoon in Brazil (Aguiar and Santos, 2018). As the temperature increased from the spring to the summer, we saw a concurrent rise in population and a rise in the number of epitokes. This trend has also been described for the congener *Alitta acutifolia* (Ehlers, 1901), previously regarded as *A. succinea*, and a proper comparison of the two species and trends would be quite relevant (Villalobos-Guerrero, 2012). Temperature has been indicated as the factor that induces metamorphosis, and this was reaffirmed by the increase in epitokes we observed during the summer and the fall (Hardege et al., 1990). We also noticed a concurrent spike of small individuals, which indicates a period of recruitment (Figure 5).

The presence of epitokes year-round indicates that the species breeds continuously, although summer and fall appear to be the seasons when most of the spawning occurs, since more epitokes were found during these periods. In the summer and fall, the number of epitokes doubles compared to what we see earlier in the year. Cohorts that are recruited during the summer likely experience a shorter lifespan because the temperature increases their development rate and reduces the time they take to reach sexual maturity (Fischer et al., 2010). Individuals recruited from the late fall to the early spring likely take longer to reach to sexual maturity, and we see larger epitokes in this period (Figure 4).

The metamorphosis of atokes in brackish water is said to be primarily induced by changes in salinity (Fong, 1991). In Galveston bay, salinity levels can vary significantly, lowering

during the spring and increasing in the summer. This change in salinity may also play a role in inducing metamorphosis in atokes. It is likely that higher temperatures, salinity increases, and extended photoperiod cues work together to induce these individuals' metamorphosis (Fong, 1991). However, since significant short-term fluctuations in salinity occur in Galveston Bay, a longer-term dataset would be necessary to properly assess the impact of salinity on *A. succinea* populations.

The changes in the number of epitokes we collected during different seasons could also have been influenced by secondary factors, such as moon phases (Kinne, 1954). On the coast of Isefjord, Denmark the spawning of

A. succinea peaks in the period leading up to the new moon (Hardege et al., 1998). In June, July, and August of 2020, samples were collected before the new moon, but during these same months in 2021, sampling occurred after the new moon. This may explain why we found a higher number of epitokes during these months in 2020 than in 2021. To improve our sampling regime in a future study, we would supplement our monthly scraping collections with simple light traps, deployed the night before the new moon during the duration of the sampling. This addition could help explain why the number of epitokes we found is much lower than those shown by previous studies (Lillie and Just, 1913; Hardege et al., 1990).

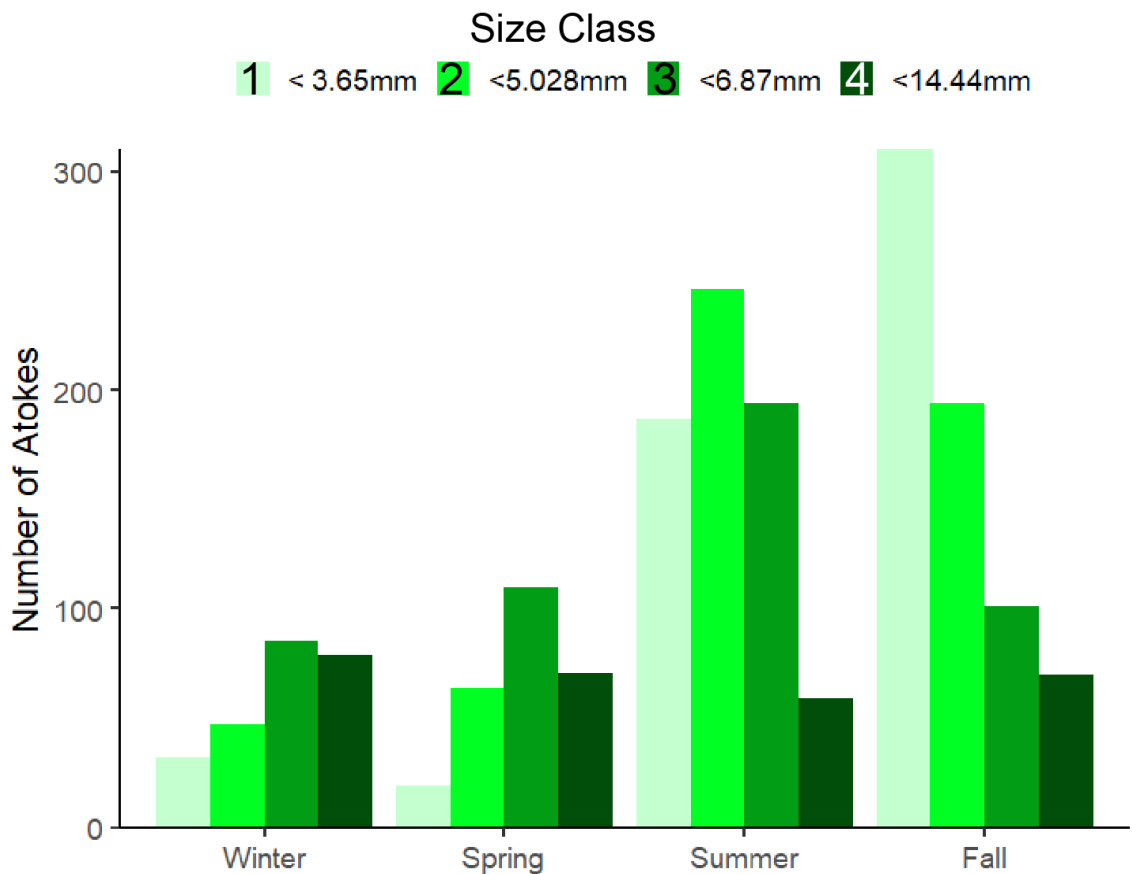


Figure 5. Variation of atoke size classes in different seasons. The peaks of size class 1 in the summer and fall indicate a period of recruitment. The size class measures are based on the length to the 20th chaetiger.

MORPHOMETRICS

The atokes we found had total lengths ranging from 1.05 mm to 52.72 mm, a substantial difference in size that is likely reflected by their ecology. To better classify atokes according to their sizes, we split them into four size classes based on the means of their length to the 20th (Figure 5). Throughout the year, the number of large atokes (size class 4) was rather consistent, whereas the numbers of size class 1 and 2 atokes peaked in the summer and winter. This also suggests the occurrence of a breeding season followed by a recruitment period in late summer and fall. Furthermore, the decrease in the number of size class 3 atokes from the summer to the fall likely happens due to sexual maturation, not to the growth of these individuals into size class 4.

We easily assigned stages to the epitokes we collected, using the system described by Aguiar and Gomes Santos (2018). However, by adding 'a clear boundary between the unmodified anterior zone and the modified posterior zone' as a prerequisite for females in stage III, we were able to determine stages more discretely. Furthermore, to categorize males, we substituted the 'presence of serrated cirri' factor (often referred to as crenulate and caused by the development of sensory papillae [Villalobos-Guerrero and Carrera-Parra, 2015]), assessed on a specific chaetiger number, by the 'degree of serration' factor. Therefore, any signs of serration were enough to differentiate Stage I males from those in Stage II, while males with highly developed serration were placed into Stage III. The quantitative analysis of morphometrics showed no significant variation in sizes, likely because not all worms were induced into metamorphosis while at the same size or segment number. Therefore, we conclude that qualitative traits are best suited for discerning epitokes' stages.

It is important to note that the sizes of the smallest and largest Stage IV males differed greatly. The smallest male had a 2.82 mm length to the 20th chaetiger and the largest had a 12.22 mm one. The smallest male was collected in October of 2020, while the largest male was collected in February of 2020. The five other largest male epitokes were collected in the winter and spring,

and the four largest females were collected in the winter, which indicates that temperature most likely drives sexual maturation at a faster rate than it drives growth.

During metamorphosis, the individuals' eyes greatly change in size. The area of an epitoke's eyes is roughly double that of a similar sized atoke. This increase in gross anatomy likely occurs due to the elongation of the rhabdomeric layer within the eyes (Miyako-Shimazaki et al., 2005). Although these individuals' eye area increases, no studies have been conducted to determine if their field of view also increases. The functionality of epitokes' eyes—whether their field of view widens and whether they can visualize more resolved images, absorb a wider spectrum of wave lengths, or see faster stimuli—remains unknown. Future work looking into the physiology of metamorphosed eyes would be necessary to determine their functional changes.

CONCLUSION

This study showed that *A. succinea* in Galveston Bay fouling communities undergo significant population fluctuations, peaking during the warmest months. Therefore, increases in water temperatures due to climate change may increase this species' expansions and northward range shifts. Given how dense the *A. succinea* population is on the Southeast Texas coast, future studies should assess its ecological interactions with other members of the fouling communities, as well as its importance in trophic levels. When analyzing different studies, we found that , the *A. succinea* population of Galveston Bay, a subtropical environment, displays an intermediate pattern compared to that of populations of different climates. Our study indicates that instead of strictly performing continuous breeding seasons, which occurs in the tropics, or punctuated breeding, which happens in temperate climates, in Galveston Bay, this species combines both approaches.

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AUTHOR CONTRIBUTIONS

M.C.H.: Conceptualization; Funding Acquisition; Project Administration; Investigation; Methodology; Visualization; Writing – original draft; Writing – review & editing;

A.S.: Conceptualization; Supervision; Resources; Methodology; Writing – review & editing.

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