# DIRECTIONAL SWIMMING VARIANCE IN SALP COLONIES MAY UNDERPIN DIEL VERTICAL MIGRATION BEHAVIOR

by

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A THESIS

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Salps are pelagic tunicates that swim with jet propulsion. Their life cycle involves a colonial stage where multiple zooids pulse asynchronously to swim. Across the 48 described salp species, there is a diversity of colony forms depending on the positioning of zooids, referred to as colony architecture. Recent work shows that swimming speed differs across architecture types, suggesting that colony architecture influences locomotion. To test whether salp species vary in their directional swimming behavior and orientation, we used in situ SCUBA-based videography to analyze swimming tortuosity (crookedness of path) and directionality (swimming angle) across colony architectures. We found that in many cases streamlined colony architectures (linear) swam straighter than less streamlined architectures (whorl). Because some salp species are strong diel vertical migrators, we also tested how swimming behavior varies with light level and found significant differences in swimming directionality between night and day. In the daytime, non-streamlined colony architectures that are considered non-migrators or shallow migrators were more common and swim angle was predominantly upward towards the surface. At night, streamlined colony architectures that are deep migrators dominated, and swim angle was predominantly downward. Our findings therefore indicate that colony architecture plays a role in diel vertical migration. Overall, we find evidence for an association between colonial morphology, diel vertical migration, and swimming behavior.

## Acknowledgements

I want to thank Kelly Sutherland for being an amazing primary thesis advisor and mentor throughout almost all my undergraduate experience. I also want to thank Casey Shoop for agreeing to be my CHC representative and teaching some of the most enjoyable and thought-provoking classes I've taken. I'd like to thank Alejandro Damian-Serrano for letting me join in on the salp speed research project and serve as a co-author, which kickstarted this entire thesis, as well as Kai Walton and Anneliese Bishop-Perdue for helping me get involved and showing me the ropes in the lab. I'd also like to thank other members of the Sutherland Lab including Terra Hiebert, Elizabeth Wallace, Farzana Yesmin, Audrey Lillie, and Will Bird for giving advice and support. Lastly, I'd like to thank my family and friends for being sources of light and encouragement in my life and giving me the drive to keep going. I'd also like to acknowledge and thank the Office of Naval Research for providing funding that made this research possible (Grant 2431J1).

# Table of Contents

# List of Figures

# List of Tables

# Introduction

Salps are gelatinous, barrel-shaped planktonic invertebrates in the phylum Chordata, subphylum Tunicata and class Thaliacea (World Register of Marine Species). As pelagic tunicates, salps swim in the water column using jet propulsion, bringing water in through a pharyngeal siphon at their anterior and then pumping it out of an atrial siphon at their posterior to propel the organism forward (Madin 1989). Salps have an alternation of generations lifecycle that involves a solitary stage where the organisms swim freely on their own as individuals as well as a colonial stage where multiple asexually budded individuals, called zooids, swim together interconnected as a unit (Anderson & Bone 1997). During the colonial stage, jet propulsion from each zooid happens asynchronously, which allows the colony to swim more efficiently and limits drag (Sutherland & Weihs 2017).

The alternation between asexual and sexual reproduction in salps allows them to reproduce efficiently. In the salp species *Soestia zonaria*, a single solitary individual can potentially bud up to 420 times (Daponte et al. 2013). Additionally, salps are highly efficient filter feeders capable of ingesting particles, including phytoplankton, bacteria and cyanobacteria, down to the submicron scale (Kremer & Madin 1992, Sutherland et al. 2010, Sutherland & Thompson 2021), and this trait combined with their rapid reproduction allows them to form large population blooms when conditions are ideal, such as during high summer water temperatures (Groeneveld et al. 2020). These population blooms can have profound effects on the surrounding ecosystem; as filter feeders, salps can accumulate small particles into larger sources of carbon, providing energy to organisms that predate on them (Fortier et al. 1994). Salps serve as food sources for a variety of organisms, including multiple fish species (Henschke et al. 2016), green

sea turtles (Sampson & Giraldo 2014) and even the little penguin *Eudyptula minor* (Cavallo et al. 2018).

Furthermore, salps provide sources of carbon to the deep sea through their fecal pellets, which sink at a rate of 2700 meters per day, a faster sinking rate than the fecal matter of any other known zooplankton (Bruland & Silver 1981). Salps also impact the ecosystem by competing with other filter feeding organisms; for example, the species *Salpa thompsoni* increasingly competitively dominate the antarctic krill *Euphausia superba* in the Western Antarctic Peninsula as ocean temperatures warm and nitrogen-phosphorous ratios shift (Plum et al. 2020, Pietzsch et al. 2023). Overall, salps play a crucial role in pelagic environments; however, challenges of keeping them in captivity, their tendency to fall apart in plankton nets and rapid digestion in predator stomachs has led them to be historically ignored and largely understudied (Henschke et al. 2016).

Currently there are 48 described species of salps, and across those species there is a diverse variety of colony forms depending on the arrangement and positioning of zooids (Damian-Serrano et al 2023, Damian-Serrano and Sutherland 2023). There are seven distinct colony architectures that arise during colony development: linear, bipinnate, cluster, whorl, oblique, transversal, and helical (Figure 1). The oblique and transversal colony architectures are understood to be the most evolutionarily ancestral, and the linear form has independently evolved three separate times, indicating that it may confer an adaptive advantage (Damian-Serrano et al. 2024).

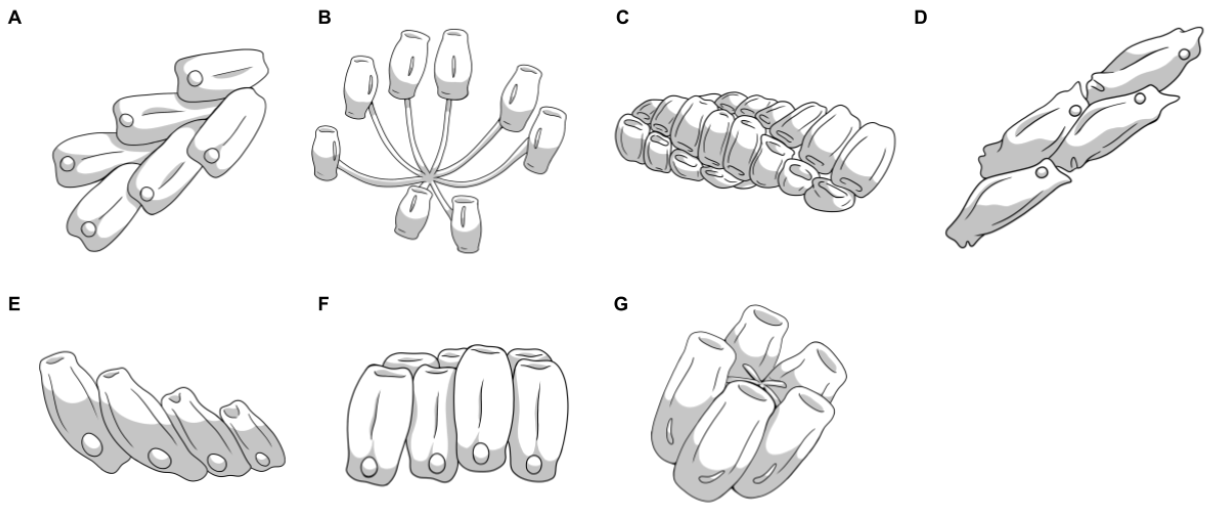


Figure 1: Types of salp colony architecture

A diagram showing the 7 types of salp colony architecture: A) Bipinnate; B) Cluster; C) Helical; D) Linear; E) Oblique; F) Transversal; G) Whorl

Swimming speed varies significantly across different salp colony architectures (Madin 1990, Sutherland and Madin 2010). Salps that have linear colony architecture, in which zooids lay almost parallel to the colony's line of motion, swim significantly faster than every other colony architecture type (Damian-Serrano et al. 2025). Additionally, the zooid angle relative relative to the stolon (the structure where budding occurs) correlates to their swimming speed: salp colonies with a smaller dorsoventral zooid-colony angle, resulting in a more streamlined build and lower jet angles, generally have faster swimming speeds. The number of zooids in a colony can also influence its speed. In salp colony architectures where the frontal area stays constant regardless of the number of zooids in the chain (linear and bipinnate), colony speed has a positive correlation with zooid count, but in architectures where the frontal area increases with the number of zooids, colony speed decreases as the number of zooids in the colony increases presumably to increased drag (Damian-Serrano et al. 2025). Salp colony architecture

demonstrably influences swimming speed, yet there has been little exploration into relationships between salp colony architecture and other aspects of swimming behavior.

Another important consideration of salp swimming behavior is that some species undertake diel vertical migration, moving from deep water in the daytime to the surface at night and returning to depth before sunrise. Some species of salps exhibit diel vertical migration to a variety of depth ranges (Stone & Steinberg 2014, Purcell & Madin 1991, Madin et al. 1996). As some salp colonies undergo daily long-distance vertical migration cycles (hundreds of meters), while others move shorter distances (30-50m) and some do not migrate at all, we expect a diversity in swimming behaviors across species, and potentially divergence in morphology to account for differences in lifestyle. We therefore predict that diel vertical migration, swimming behavior, and the colony architecture of a salp colony are all interlinked.

In this study, we used a video library of salp colonies swimming *in-situ* to determine diel vertical migration behavior for each species, based on their presence at the surface in daytime videos versus nighttime videos. Video analysis was also used to calculate the tortuosity (crookedness) of a salp colony's swimming path and the angle of swimming direction relative to the surface. We compared these metrics of swimming behavior across colony architecture types, across species, between migrating and non-migrating salp species, and between videos taken in the daytime and at night. In total, the study involved 15 salp species, 5 salp colony architectures, and 164 total measured videos.

# Methods

Video footage of salps *in situ* were recorded by members of the Sutherland Lab during SCUBA dives off the coast of Kailua-Kona (Hawai'i Big Island, 19°42′38.7″ N, 156°06′15.8″ W) using a variety of camera systems including a darkfield stereography system (Sutherland et. al. 2024). Additional video footage was recorded near West Palm Beach, FL and the Pacific coast of Panama in Coiba National Park. The resulting salp video library was shared between this study and a previous study investigating salp swimming speed (videography methods described in Damian-Serrano et al. 2025). Of the videos used in this study, 91 were recorded in Kona, 37 in West Palm Beach, and 36 in Panama.

**Video Analysis**

In the previous study, 3D stereoscopic videos were measured using EventMeasure (SeaGIS) software to record the xyz positions of swimming salp colonies over time (typically measured about 10 times every 0.166 seconds). These xyz values were stored in txt files that were then reanalyzed for this current study.

The 2D videos were imported and subsequently analyzed using the FFMPEG plugin in ImageJ. The xy position of the salp colony was recorded every 0.166 seconds of video 10 times to keep consistent with the length of stereoscopic video measurements, resulting in a window of 1.66 seconds. The tip of the first zooid in the colony or a viscera visible inside a zooid was used as a landmark and kept consistent for each frame. In the same frame a non-moving particle, typically a piece of detritus or small organism, was used as a reference point to control for movement of the water and camera. The 1.66 second window of time to measure the salp's position was haphazardly selected for visual clarity and the presence of a reference particle in frame.

In total, position data was recorded from 164 videos representing 15 different salp species and 5 colony architectures. For each video, the swimming tortuosity and swimming direction were recorded, as well as whether the video was taken in the daytime (bluewater) or nighttime (blackwater). Day/night counts were also recorded using videos that had a swimming salp but were too blurry or shaky to properly measure as a means of increasing sample size for each species. A qualitative comparison of day and night counts was used to test whether species previously observed to vertically migrate have a higher presence at the surface in the nighttime than the daytime, with non-migrators present at the surface about equally in the daytime and nighttime.

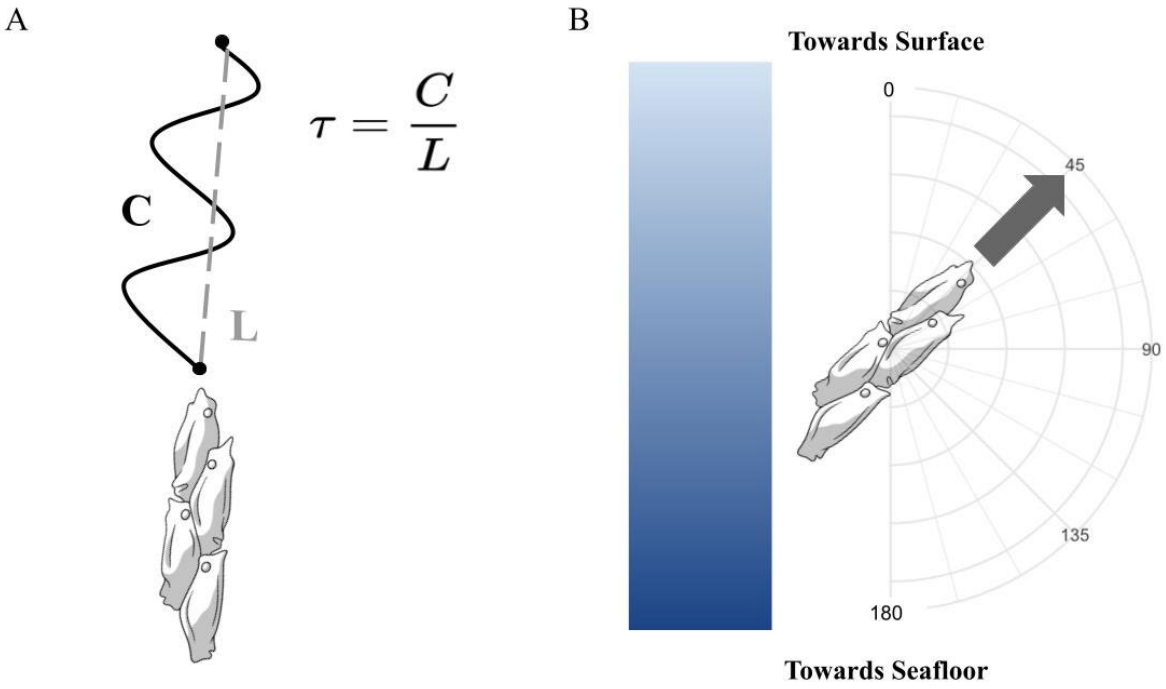


Figure 2: Salp tortuosity and Swimming Direction

(Panel A) Diagram showing how swimming tortuosity was determined based on the total distance (C) and net displacement (L) of the salp chain. (Panel B) Diagram showing the orientation of the angle measurements, where a measure of 0 degrees was swimming towards the surface of the water and a measure of 180 degrees was swimming towards the seafloor.

## Tortuosity Calculations

Swimming tortuosity (crookedness of path) was calculated from the xyz and xy positions of salps over time using the simple equation $\tau = \frac{C}{L}$, where C is the total distance traveled from start to end (gross displacement) and L is the shortest possible distance from start to end (net displacement) (Figure 2). The resulting tortuosity value is a number greater than or equal to 1, where 1 is a measure of perfectly straight swimming and increasing values indicate decreasing path straightness.

The net displacement was calculated over the 1.66 second window using the equation $\sqrt{(x_{ref} - x)^2 + (y_{ref} - y)^2 + (z_{ref} - z)^2}$, where $x_{ref}$, $y_{ref}$, and $z_{ref}$ are the coordinates of the reference point and x, y and z are the coordinates of the salp's position for each dimension respectively. The total distance was calculated by summing the displacements between each 0.166 second measurement. Next, total distance was divided by net displacement to calculate the swimming tortuosity of the salp.

**Angle Calculations**

Salp swimming direction was calculated by taking the difference of adjacent relative coordinates and dividing that difference by the time between them (0.166 seconds) to create the vectors U and W for x and y respectively. In total, 9 U and 9 W vectors were calculated for each video. The equation ATAN2(U, W) was used to calculate the angle between these 2 vectors (the swimming angle).

Swimming angles (mean of n=9 for each video) were calculated based on U and W velocities at each time step (t=0.166 seconds) where angle equals ATAN2(U, W). The angle was converted to positive degrees, shifted 90 degrees counterclockwise, and condensed to a range of 0-180 degrees so that an angle of 0 degrees corresponded to vertical swimming directly upward toward the surface while 180 degrees corresponded to directly downward swimming away from the surface.

**Software**

Data wrangling, tortuosity, and angle calculations were done in Google Sheets. R Studio version 4.3.1 (2023-06-16) was used for statistical tests, including ANOVA, Tukey's HSD post hoc test, and Welch Two-Sample t-tests. The R Studio package 'circular' was used for statistical

tests involving circular data such as Watson's Test for Circular Uniformity and Watson's Two-Sample Test for Circular Homogeneity. The R Studio packages 'ggplot2', 'patchwork' and 'viridis' were used for help creating plots.

# Results

The abundance of colonies at the surface between day and night differed across different salp species. Swimming behavior also varied across salp species and colony architectures. These differences were more pronounced for swimming tortuosity than for swimming directionality. Additionally, swimming behavior varied across species with different diel vertical migration behaviors and migration depth ranges. Lastly, there appeared to be different swimming behaviors between the day and night as well as a shift in the abundance of migrating species on the surface.

## Day/Night Counts

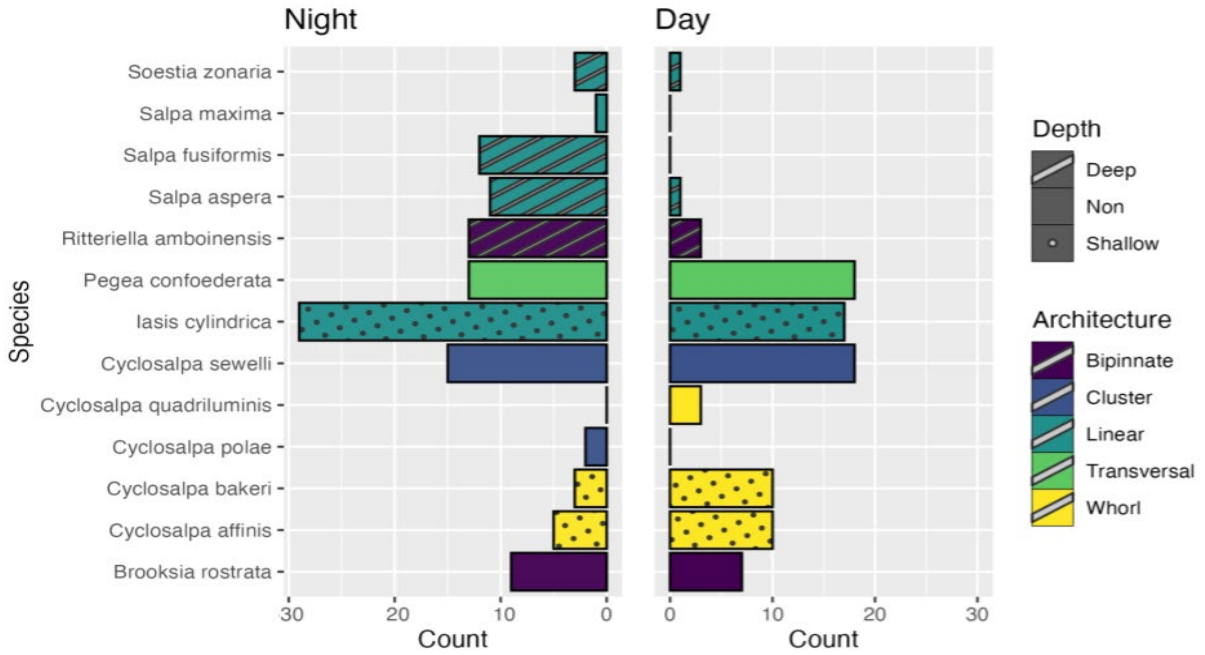


Figure 3: Salp Species Counts in Day Versus Night

Counts of salp species in night (left) versus day (right). Salp colony architectures are represented using different colored bars and the DVM depth range based on data from the literature is indicated by the shading texture on the bar.

We predicted that salp species previously described to vertically migrate would have a greater occurrence on the surface at night than in the daytime, while species that are not known to migrate will be seen equally during both day and night. When comparing the presence of different salp species in the nighttime and the daytime (Figure 3), the species *Soestia zonaria*, *Salpa fusiformis*, *Salpa aspera*, and *Ritteriella amboinensis* all occurred more frequently at night than during the daytime (their total N is >80% at night). The salp species *Cyclosalpa sewelli*, *Brooksia rostrata*, *Pegea confoederata*, *Cyclosalpa bakeri*, and *Cyclosalpa affinis* were present during both day and night (40 - 60% night).

## Swimming Tortuosity

*Tortuosity Comparison Across Architectures*

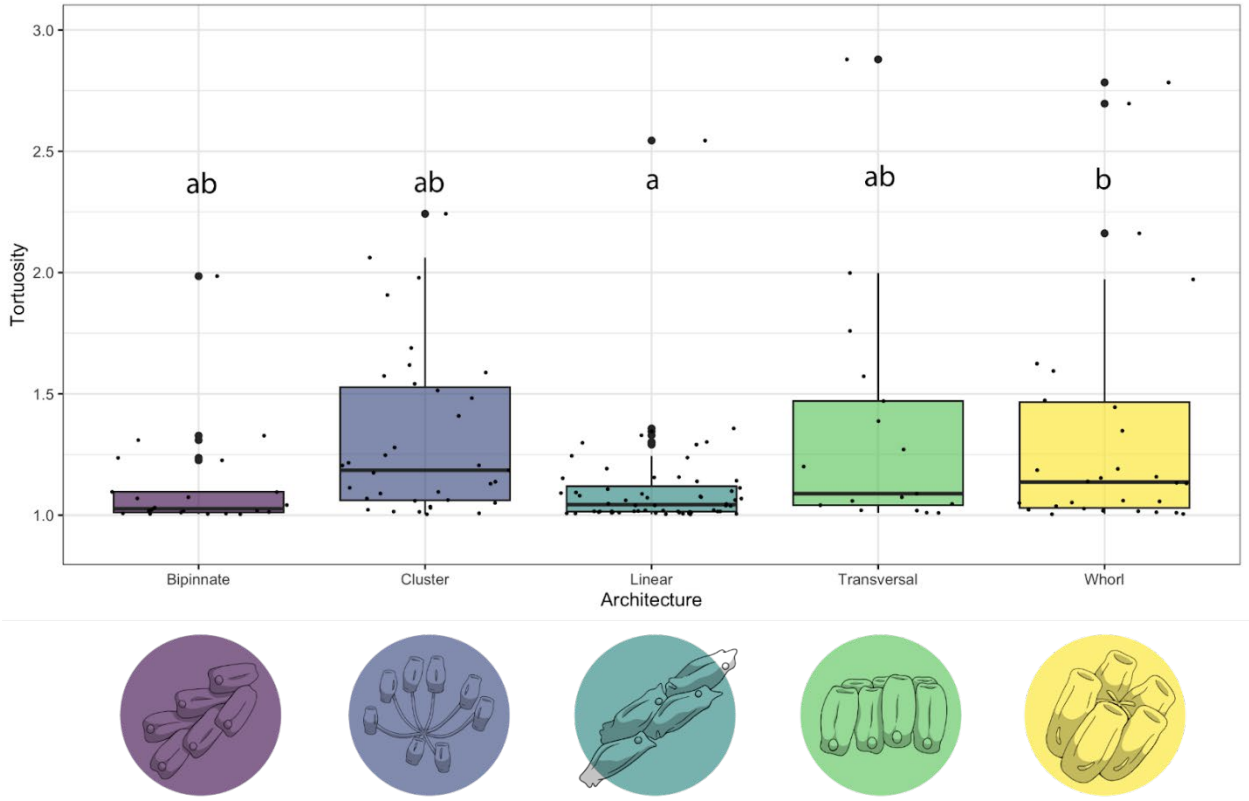


Figure 4: Tortuosity Across Salp Architectures

Distribution of swimming tortuosity across five salp colony architectures. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N = 22, 35, 60, 17, 30).

When comparing swimming tortuosity across salp colony architectures, linear colonies had significantly lower tortuosity (i.e. swam in a straighter path) than whorl colonies (ANOVA, df = 4, F-value = 3.82, p-value < 0.01) (Figure 4). The other colony architectures (Bipinnate, Cluster, Transversal) were not significantly different from one another but had tortuosities that were higher than Linear but lower than Whorl (Table 1).

| Architecture | Average Tortuosity | Standard Deviation | Sample Size |
|---|---|---|---|
| Bipinnate | 1.119 | 0.218 | 22 |
| Cluster | 1.316 | 0.337 | 35 |
| Linear | 1.109 | 0.213 | 60 |
| Transversal | 1.347 | 0.493 | 17 |
| Whorl | 1.464 | 0.879 | 30 |

Table 1: Tortuosity Across Colony Architecture Groups

*Tortuosity Across Diel Vertical Migration Behaviors*

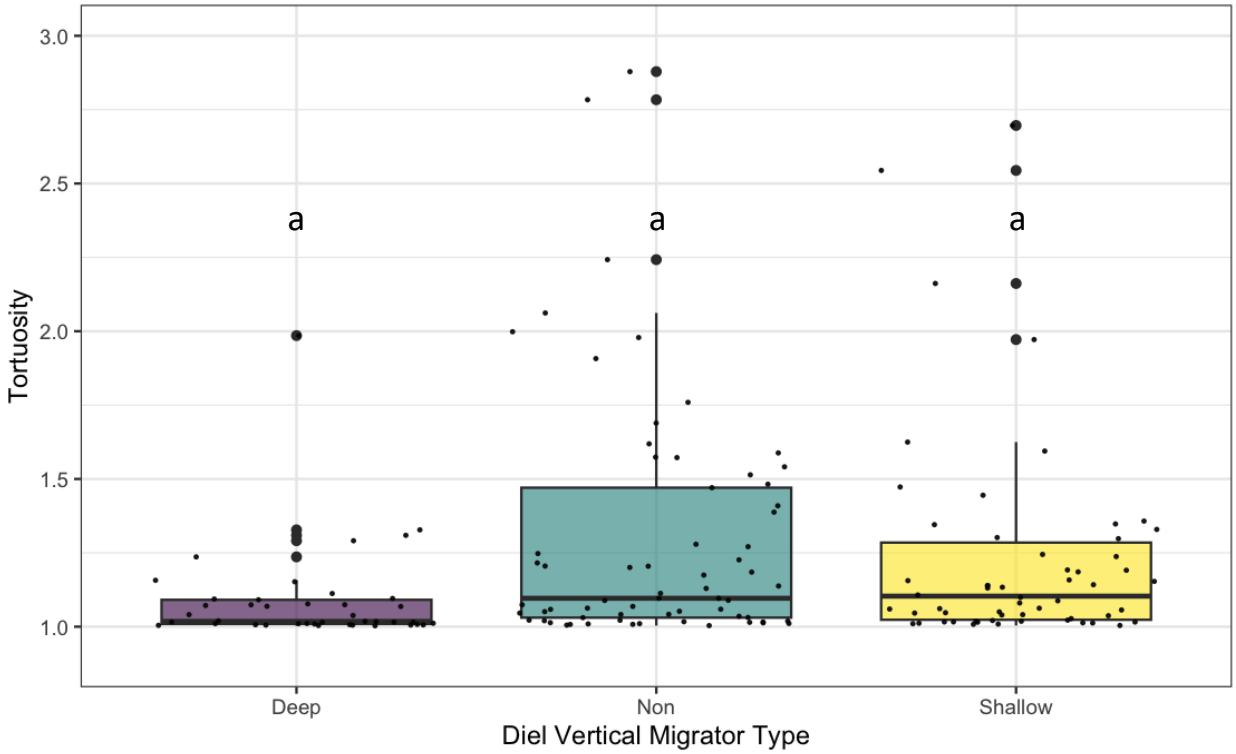


Figure 5: Tortuosity Across Diel Vertical Migration Depth Groups

Swimming tortuosity across different behaviors of diel vertical migration. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N = 41, 58, 65).

Salps that undergo vertical migration did not swim straighter than salp species known not to be vertical migrators (ANOVA, df = 1, F-value = 1.303, p-value = 0.255). Additionally, there were only marginally significant differences in tortuosity when comparing deep migrating salp species (>50m), shallow migrators (<50m), and non-migrators (ANOVA, df = 2, F-value = 3.018, p-value = 0.0517) (Figure 5). However, deep migrators swam straighter than shallow migrators when compared directly (Welch two-sample t-test, df = 67.49, test statistic = -2.3478, p-value < 0.05). Across species, the shallowly-migrating whorl salp species *Cyclosalpa bakeri*

swam more crookedly than the deep-migrating linear salp species *Salpa aspera* and *Salpa fusiformis,* the shallow-migrating linear *Iasis cylindrica*, and the bipinnate salp species *Brooksia rostrata* (ANOVA, df = 14, F-value = 2.21, p-value < 0.01).

| Migration Behavior | Average Tortuosity | Standard Deviation | Sample Size |
|---|---|---|---|
| All DVM Species | 1.210 | 0.518 | 99 |
| Deep | 1.088 | 0.168 | 41 |
| Shallow | 1.300 | 0.646 | 58 |
| Non DVM Species | 1.300 | 0.411 | 65 |

Table 2: Tortuosity Across DVM Behavior Types

| Species | Average Tortuosity | Standard Deviation | Sample Size |
|---|---|---|---|
| *Brooksia rostrata* | 1.048 | 0.068 | 10 |
| *Cyclosalpa affinis* | 1.194 | 0.259 | 14 |
| *Cyclosalpa bakeri* | 1.721 | 1.209 | 13 |
| *Cyclosalpa polae* | 1.359 | 0.324 | 2 |
| *Cyclosalpa quadriluminis* | 1.614 | 1.013 | 3 |
| *Cyclosalpa sewelli* | 1.313 | 0.343 | 33 |
| *Iasis cylindrica* | 1.164 | 0.280 | 31 |
| *Pegea confoederata* | 1.267 | 0.309 | 15 |
| *Pegea sp.* | 1.949 | 1.314 | 2 |
| *Ritteriella amboinensis* | 1.180 | 0.301 | 10 |
| *Ritteriella sp.* | 1.167 | 0.227 | 2 |
| *Salpa aspera* | 1.036 | 0.041 | 12 |
| *Salpa fusiformis* | 1.040 | 0.045 | 12 |
| *Soestia zonaria* | 1.063 | 0.065 | 4 |
| *Salpa maxima* | 1.290 | N/A | 1 |

Table 3: Tortuosity Across Salp Species

*Comparison of Tortuosity Between DVM Depth Categories within Colony Architecture Groups*

Among salps that have linear colony architecture, species that have a deep diel vertical migration range (*Salpa* spp.) swam straighter than species that have a shallow vertical migration range (*I. cylindrica*) (ANOVA, df = 1, F-value = 4.572, p-value < 0.05) (Figure 6). Within the bipinnate architecture category, there were no significant differences in tortuosity between non-migrating species and deep migrators (ANOVA, df = 1, F-value = 2.023, p-value = 0.1703). No other colony architectures have both deep and shallow migrating species represented, or exhibit no diel vertical migration behavior at all, so no further comparisons could be made within architectures.

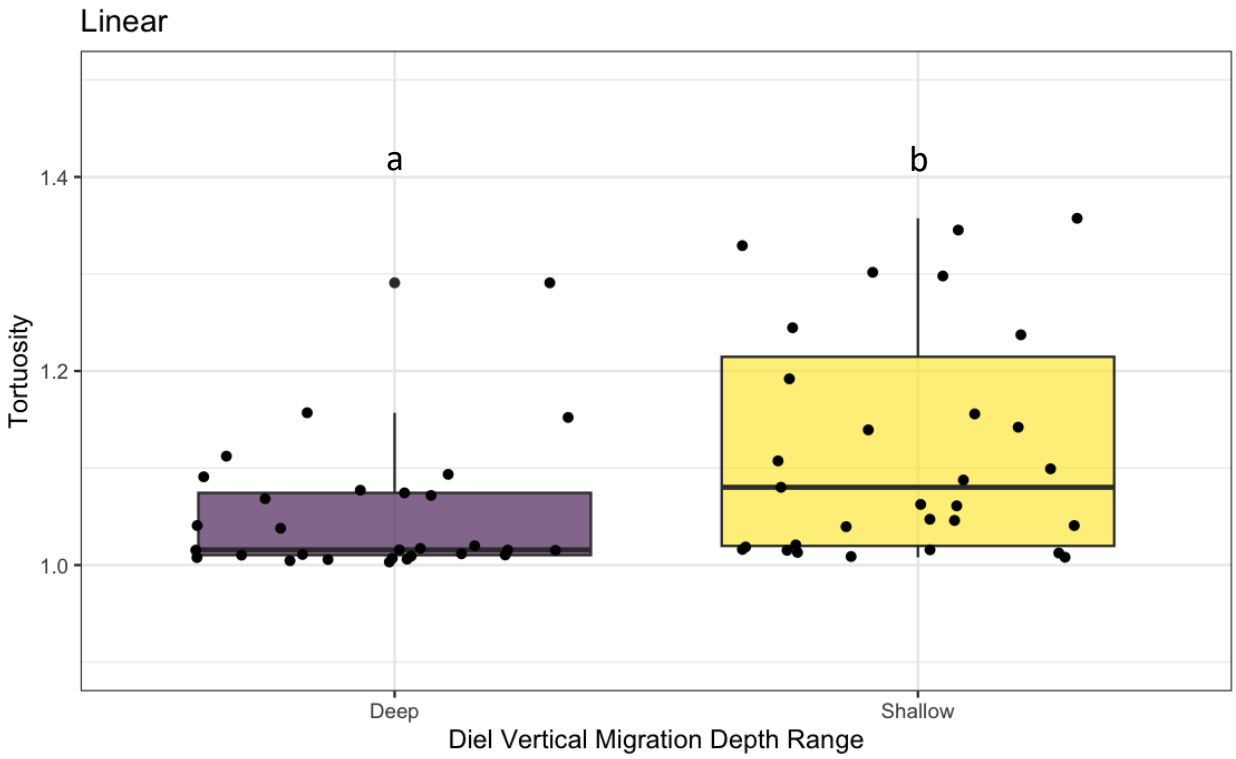


Figure 6: Tortuosity of Depth Groups of Linear Architecture

Swimming tortuosity across different behaviors of diel vertical migration (DVM) within only the Linear colony architecture group. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N = 29, 31)

*Tortuosity Comparisons Between Night and Day*

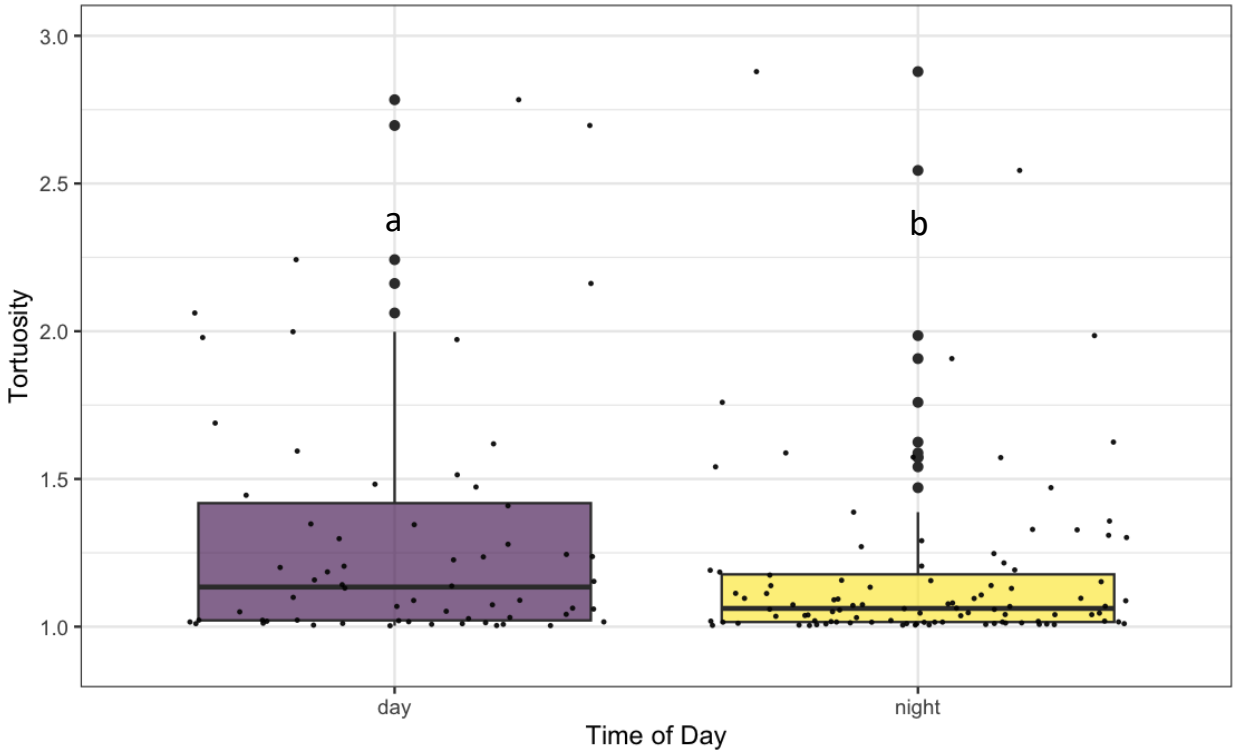


Figure 7: Tortuosity By Time of Day

Swimming tortuosity across samples taken in the daytime and samples taken in the nighttime. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N = 29, 31)

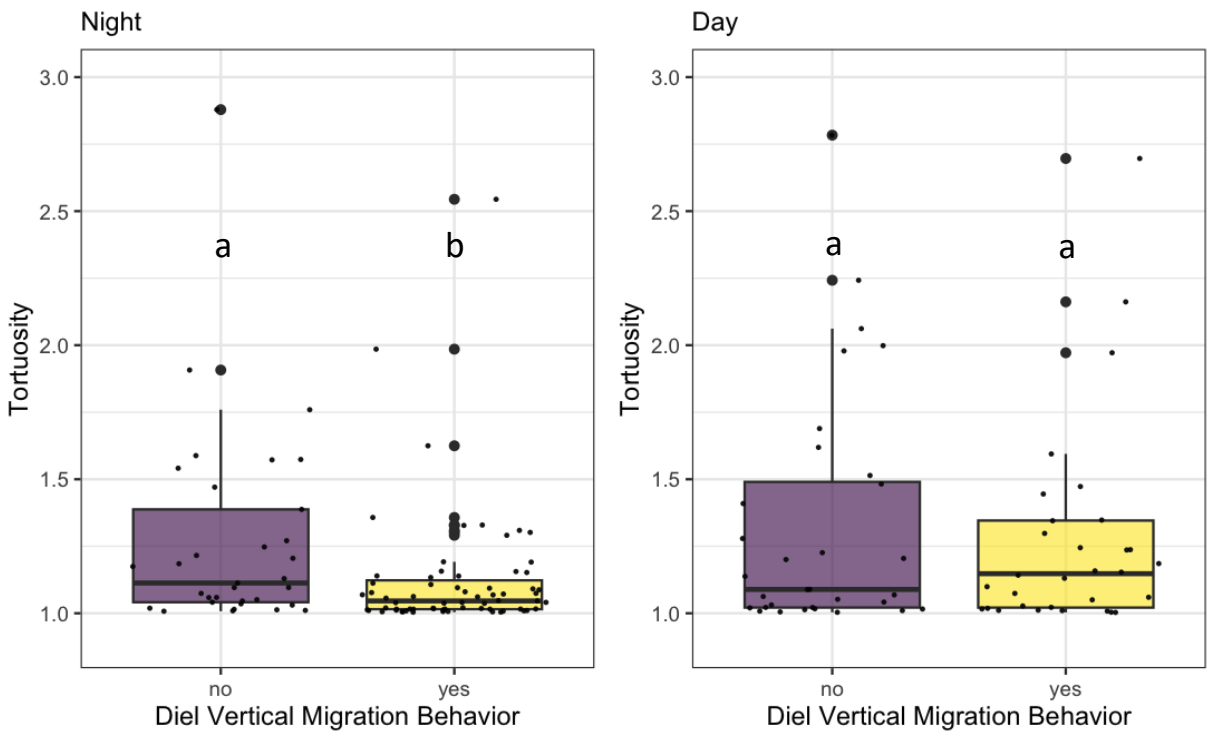


Figure 8: Tortuosity Between Night and Day and Across DVM Behaviors

Boxplots showing the distributions in tortuosity between salp species that exhibit diel vertical migration and salps that do not migrate, separated into the categories of samples taken at night and in the day. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N = 33, 67, 32, 32)

Comparisons between night and day are important for understanding diel vertical migration behavior because DVM causes migratory species to be much more present at the surface at night. Additionally, changes in light level may trigger different swimming behaviors in migratory species. Between salp videos taken in the daytime (bluewater) and the nighttime (blackwater), salps had lower tortuosity as a whole at night than in the day (ANOVA, df = 1, F-value = 6.32, p-value < 0.05) (Figure 7).

During the nighttime, salp species with diel vertical migration behavior swam straighter than non-migrators (Welch Two Sample T-Test, df = 44.731, test-statistic = -2.0522, p-value <

0.05), but in the daytime there were no significant differences in tortuosity between migrators and non-migrators (Welch Two Sample T-Test, df = 48.072, test-statistic = 0.41835, p-value = 0.6776) (Figure 8).

Among samples taken at night, salps with linear colony architecture swam straighter than transversal colonies (ANOVA, df = 4, F-value = 2.677, p-value < 0.05), while samples taken in the daytime had no significant differences in tortuosity across different colony architectures (ANOVA, df = 4, F-value = 1.204, p-value = 0.985) (Figure 9). Within each architecture group, there were no differences in tortuosity between day and night.

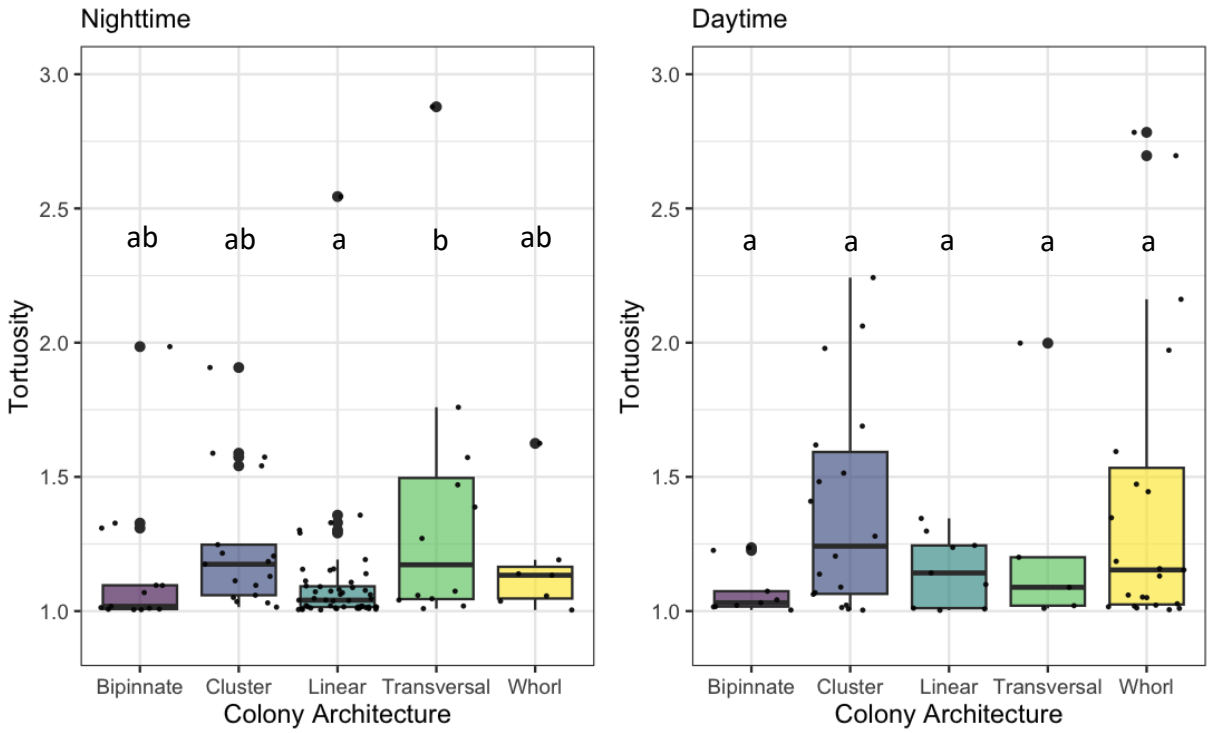


Figure 9: Tortuosity Across Architectures Separated into Day and Night

Boxplots showing the distribution in tortuosity across different salp colony architectures, separated into nighttime and daytime. The horizontal center line indicates the median, the colored box range indicates the first and third quartiles, and the vertical line represents 1.5 times the interquartile range. Groups with significant differences between them are labeled with distinct letters (N Night = 13, 17, 51, 12, 7; N Day = 9, 18, 9, 5, 23)

## Swimming Directionality

### *Directionality Across Colony Architectures*

Across different salp colony architectures, swimming was directional (non-uniform) for the Linear, Cluster, and Transversal groups, and random for Whorl and Bipinnate groups (Table 4). There were no significant differences between architectures in the angle of swimming direction (ANOVA, df = 4, F value = 0.701, p-value = 0.593) (Figure 10). Of the three colony architecture groups that did swim directionally, there were no significant differences in angle distribution when compared between architectures using Watson's Two-Sample Test of Homogeneity (Table 5).

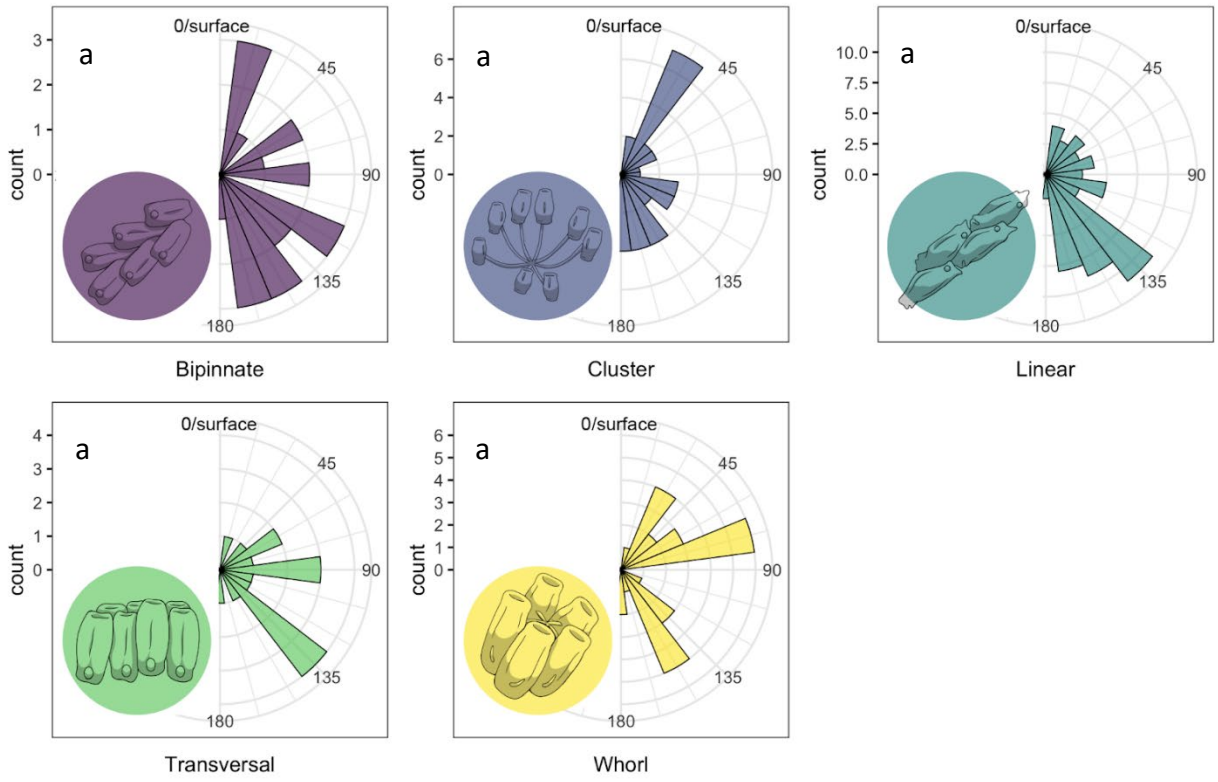


Figure 10: Swimming Directionality of Colony Architecture Groups

Semicircular histograms showing swimming angle measurements across different salp colony architectures, where a measure of zero degrees means directly vertical upwards swimming towards the surface of the water column and a measure of 180 degrees means vertical downwards swimming (N = 20, 35, 60, 22, 28)

| Architecture | Watson Test p-value | Watson Test Statistic | Average Angle (Degrees) | N |
|---|---|---|---|---|
| Bipinnate | > 0.10 | 0.1067 | 100.6936353 | 22 |
| Cluster | **< 0.01** | 0.4401 | 101.9002566 | 35 |
| Linear | **< 0.01** | 0.4096 | 108.2766964 | 60 |
| Transversal | **< 0.01** | 0.3534 | 94.92348248 | 17 |
| Whorl | > 0.10 | 0.0951 | 89.0482908 | 30 |

Table 4: Watson's Test for Circular Uniformity Across Salp Colony Architectures

| Comparison | Watson Two Test Statistic | Watson Two Test p-value |
|---|---|---|
| Linear-Cluster | 0.1355 | > 0.10 |
| Linear-Transversal | 0.0558 | > 0.10 |
| Transversal-Cluster | 0.1326 | > 0.10 |

Table 5: Watson's Two-Sample Test of Uniformity Across Directional Salp Colony Architectures

*Swimming Directionality Across DVM Depth Ranges*

Across salp species with different depth ranges of diel vertical migration as well as for non-migratory species, there was significant directional swimming (Table 6). However, there were no significant differences in the angle of swimming direction between groups (ANOVA, df = 2, F value = 0.621, p-value = 0.0517). There were also no significant differences in the distribution of angles between the different categories of migration behavior (Table 7).

| Migration Behavior | Watson Test Statistic | Watson Test p-value |
|---|---|---|
| Shallow Migratory Species (<50m) | 1.0979 | **< 0.01** |
| Deep Migratory Species (>50m) | 1.0151 | **< 0.01** |
| All Migratory Species | 0.5376 | **< 0.01** |
| Non-Migratory Species | 1.2697 | **< 0.01** |

Table 6: Watson's Test for Circular Uniformity for Different DVM Behaviors

| Comparison | Watson Two Test Statistic | Watson Two Test p-value |
|---|---|---|
| Deep - Shallow | 0.0844 | > 0.10 |

| | | |
|---|---|---|
| Deep - Non | 0.0967 | > 0.10 |
| Shallow - Non | 0.0519 | > 0.10 |

Table 7: Watson's Two-Sample Test of Uniformity Comparing DVM Behaviors (Note: statistical test used does not provide exact p-values)

*Swimming Directionality Across DVM Depth Ranges within Architecture Groups*

Similarly to the tortuosity comparison, linear and bipinnate were the only architecture groups with species that have more than one type of DVM behavior represented: deep (*Soestia zonaria*, *Salpa fusiformis*, *Salpa aspera*) and shallow-range (*Iasis cylindrica*) migration for linear, and deep (*Riteriella amboinensis*) and non-migration (*Brooksia rostrata*) for bipinnate. Within the linear architecture group, there was no difference in the swim angle between the deep and shallow DVM species (ANOVA, df = 1, F value = 0.098, p-value = 0.657). Additionally, there was no significant difference in the distribution of angles between deep and shallow (Watson's Two-Sample Test of Homogeneity, test statistic = 0.0414, p-value > 0.1).

As for the Bipinnate architecture group, there were no significant differences in the average angle between non-migrators and deep-range migrators (ANOVA, df = 1, F value = 0.307, p-value = 0.586). There were also no significant differences in the angle distribution between deep-range and non-migrators (Watson's Two-Sample Test of Homogeneity, test statistic = 0.0686, p-value > 0.1).

*Swimming Directionality and Light Level*

Daytime videos and nighttime videos both had significant directionality (Table 8). Between videos taken in the daytime versus taken at night, there was a significant difference in the average swimming angle (ANOVA, df = 1, F value = 9.327, p value < 0.01). Additionally, there was a significant difference in the distribution of angles between day and night (Watson's

Two-Sample Test of Homogeneity, test statistic = 0.218, p-value < 0.05). The majority of samples taken at night were linear (N = 51), followed by cluster (N = 17), and bipinnate (N = 13). The majority of samples taken in the daytime were whorl (N = 23) and cluster (N = 18) (Figure 11).

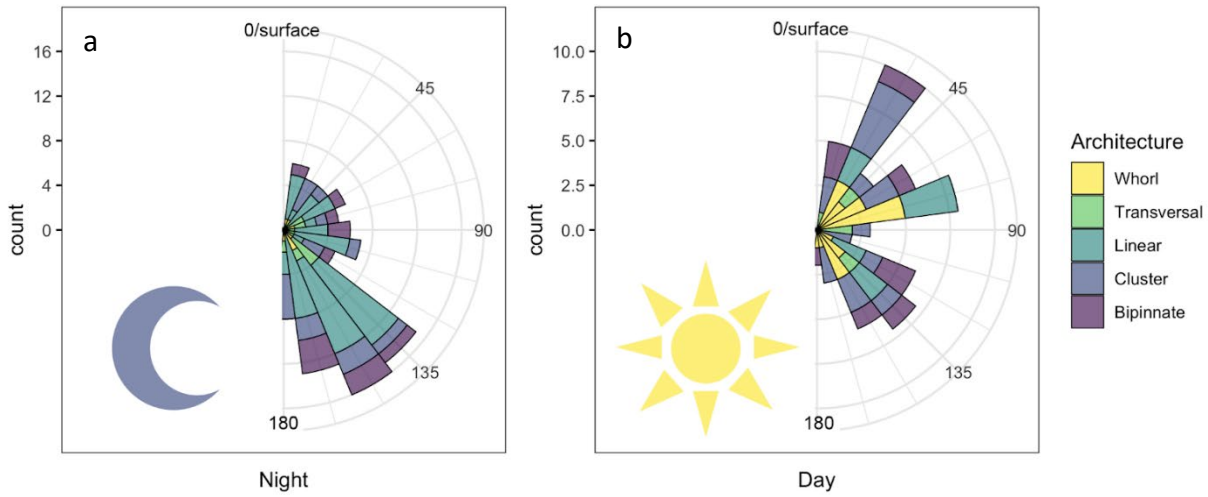


Figure 11: Swimming Directionality of Day and Night Showing Distribution of Colony Architectures

Semicircular histograms showing frequency of swimming angle measurements of samples taken in the daytime and nighttime. where a measure of zero degrees means directly vertical upwards swimming towards the surface of the water column and a measure of 180 degrees means vertical downwards swimming. Distribution of salp colony architectures are represented by different bands of colors within the bars of the histogram (N = 100, 64)

| Time | Watson Test Statistic | Watson Test p-value |
|---|---|---|
| Day | 0.4246 | **< 0.01** |
| Night | 0.8585 | **< 0.01** |

Table 8: Watson's Test for Circular Uniformity for Samples Taken at Day and Night

| Architecture of Day-Night Comparison | T-Test df | T-Test Statistic | T-Test p-value |
|---|---|---|---|
| Bipinnate | 15.996 | 0.51271 | 0.6152 |
| Cluster | 32.742 | -1.9299 | 0.06232 |
| Linear | 13.338 | -1.629 | 0.1415 |
| Transversal | 7.2825 | 1.0002 | 0.3493 |
| Whorl | 8.651 | 0.7562 | 0.4696 |

Table 9: Welch Two Sample t-test Comparing Day and Night Average Swimming Angle for Colony Architectures

There were no significant differences in average swimming direction between colony architectures during nighttime only (ANOVA, df = 4, F value = 0.274, p-value > 0.5). Additionally, in the daytime there were no differences in the average swimming direction between colony architectures (ANOVA, df = 4, F value = 0.091, p-value = 0.985). There were also no significant differences in swimming direction between day and night for any specific architecture groups (Table 9).

We split the samples taken in the daytime and nighttime into subcategories of species that exhibit diel vertical migration and those that do not, creating 4 subcategories (Figure 12). Each of these subcategories exhibited significant directionality (Table 12), but were not significantly different from one another in terms of angle distribution (Table 10). Vertically migrating species had differences in swim angle between day and night with a more downward angle during the night. Non-migratory species showed no significant differences in swim angle between day and night samples (Table 11).

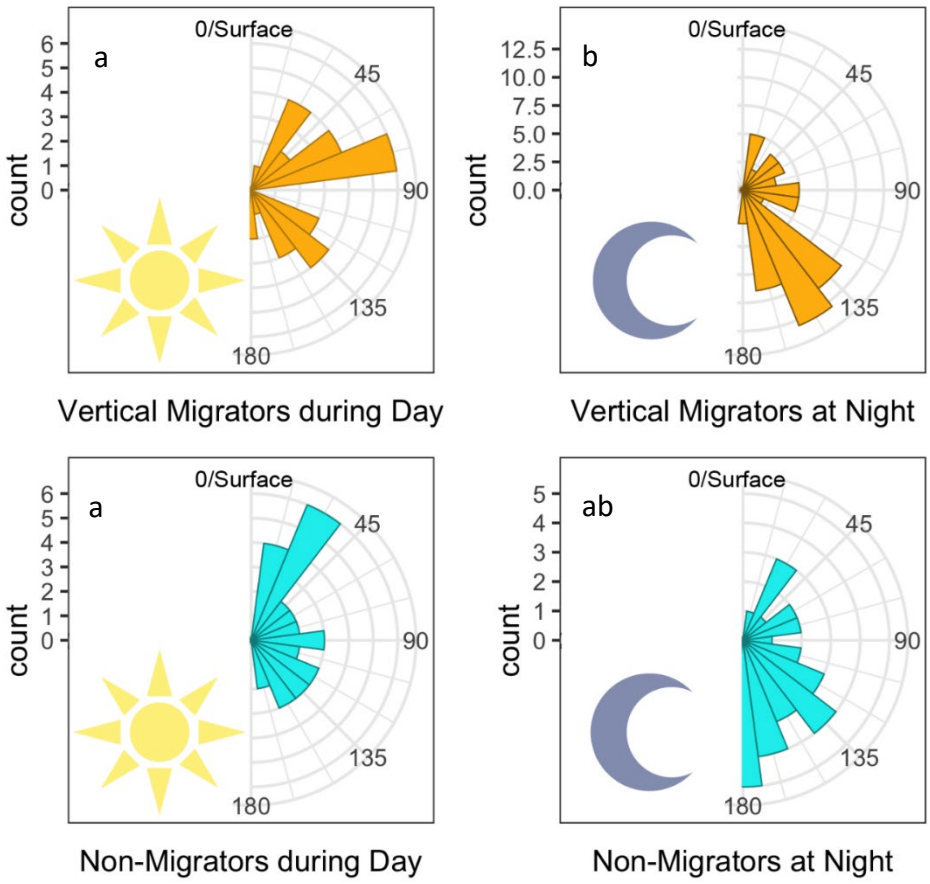


Figure 12: Directionality Between Vertical Migrators and Time of Day

Semicircular histograms showing frequency of swimming angle measurements for species that exhibit diel vertical migration and non-migratory species in both night and day, where a measure of zero degrees means directly vertical upwards swimming towards the surface of the water column and a measure of 180 degrees means vertical downwards swimming (N = 32, 67, 32, 33)

| Comparison | Watson Two-Sample Test Statistic | Watson Two-Sample Test p-value |
|---|---|---|
| Day Migrators - Day Non-Migrators | 0.0388 | > 0.10 |
| Night Migrators - Night Non-Migrators | 0.107 | > 0.10 |
| Day Migrators - Night Migrators | 0.1358 | > 0.10 |

| | | |
|---|---|---|
| Day Non-Migrators - Night Non-Migrators | 0.1021 | > 0.10 |

Table 10: Watson's Two-Sample Test of Homogeneity Comparing Migratory and Non-migratory Salp Angle Distribution Across Day and Night

| Comparison | T-test df | T-test Test Statistic | T-test Two-Sample Test p-value |
|---|---|---|---|
| Day Migrators - Day Non-Migrators | 62 | 0.34541 | 0.731 |
| Night Migrators - Night Non-Migrators | 57.023 | 0.10046 | 0.9203 |
| Day Migrators - Night Migrators | 59.393 | -2.1357 | **0.03683** |
| Day Non-Migrators - Night Non-Migrators | 62.725 | -1.9879 | 0.05119 |

Table 11: Welch Two-Sample Test Comparing Migratory and Non-migratory Salp Average Direction Across Day and Night

| Migration Behavior and Time | Watson Test Statistic | Watson Test p-value |
|---|---|---|
| Day Migrators | 0.1993 | **< 0.05** |
| Night Migrators | 0.5003 | **< 0.01** |
| Day Non-Migrators | 0.2621 | **< 0.025** |
| Night Non-Migrators | 0.4501 | **< 0.01** |

Table 12: Watson's Test for Circular Uniformity for Migrators and Non-Migrators During Day and Night

**Supplemental Tables**

| Comparison | TukeyHSD p-value |
|---|---|
| Cluster-Bipinnate | 0.520 |
| Linear-Bipinnate | 1.000 |
| Transversal-Bipinnate | 0.543 |
| Whorl-Bipinnate | 0.064 |
| Linear-Cluster | 0.222 |
| Transversal-Cluster | 1.000 |
| Whorl-Cluster | 0.696 |
| Transversal-Linear | 0.332 |
| Whorl-Linear | **0.007** |
| Whorl-Transversal | 0.920 |

Table 13: Tortuosity Comparisons Across Colony Architectures

| Comparison | TukeyHSD p-value |
|---|---|
| Cluster-Bipinnate | 0.897 |
| Linear-Bipinnate | 0.982 |
| Transversal-Bipinnate | 0.265 |
| Whorl-Bipinnate | 1.000 |
| Linear-Cluster | 0.385 |
| Transversal-Cluster | 0.712 |
| Whorl-Cluster | 0.977 |
| Transversal-Linear | **0.024** |
| Whorl-Linear | 0.976 |
| Whorl-Transversal | 0.528 |

Table 14: Tortuosity Comparisons Across Colony Architectures (Night Only)

| Comparison | TukeyHSD p-value |
|---|---|
| *Cyclosalpa affinis-Brooksia rostrata* | 1.00 |
| *Cyclosalpa bakeri-Brooksia rostrata* | **0.040** |
| *Cyclosalpa polae-Brooksia rostrata* | 1.00 |
| *Cyclosalpa quadriluminis-Brooksia rostrata* | 0.853 |
| *Cyclosalpa sewelli-Brooksia rostrata* | 0.952 |
| *Iasis cylindrica-Brooksia rostrata* | 1.00 |
| *Pegea confoederata-Brooksia rostrata* | 0.997 |
| *Pegea sp.-Brooksia rostrata* | 0.404 |
| *Ritteriella amboinensis-Brooksia rostrata* | 1.00 |
| *Ritteriella sp.-Brooksia rostrata* | 1.00 |
| *Salpa aspera-Brooksia rostrata* | 1.00 |
| *Salpa fusiformis-Brooksia rostrata* | 1.00 |
| *Salpa maxima-Brooksia rostrata* | 1.00 |
| *Soestia zonaria-Brooksia rostrata* | 1.00 |
| *Cyclosalpa bakeri-Cyclosalpa affinis* | 0.159 |
| *Cyclosalpa polae-Cyclosalpa affinis* | 1.00 |
| *Cyclosalpa quadriluminis-Cyclosalpa affinis* | 0.981 |
| *Cyclosalpa sewelli-Cyclosalpa affinis* | 1.00 |
| *Iasis cylindrica-Cyclosalpa affinis* | 1.00 |
| *Pegea confoederata-Cyclosalpa affinis* | 1.00 |
| *Pegea sp.-Cyclosalpa affinis* | 0.663 |
| *Ritteriella amboinensis-Cyclosalpa affinis* | 1.00 |
| *Ritteriella sp.-Cyclosalpa affinis* | 1.00 |
| *Salpa aspera-Cyclosalpa affinis* | 1.00 |
| *Salpa fusiformis-Cyclosalpa affinis* | 1.00 |

| | |
|---|---|
| *Salpa maxima-Cyclosalpa affinis* | 1.00 |
| *Soestia zonaria-Cyclosalpa affinis* | 1.00 |
| *Cyclosalpa polae-Cyclosalpa bakeri* | 1.00 |
| *Cyclosalpa quadriluminis-Cyclosalpa bakeri* | 1.00 |
| *Cyclosalpa sewelli-Cyclosalpa bakeri* | 0.289 |
| *Iasis cylindrica-Cyclosalpa bakeri* | **0.022** |
| *Pegea confoederata-Cyclosalpa bakeri* | 0.353 |
| *Pegea sp.-Cyclosalpa bakeri* | 1.00 |
| *Ritteriella amboinensis-Cyclosalpa bakeri* | 0.241 |
| *Ritteriella sp.-Cyclosalpa bakeri* | 0.955 |
| *Salpa aspera-Cyclosalpa bakeri* | **0.018** |
| *Salpa fusiformis-Cyclosalpa bakeri* | **0.020** |
| *Salpa maxima-Cyclosalpa bakeri* | 1.00 |
| *Soestia zonaria-Cyclosalpa bakeri* | 0.424 |
| *Cyclosalpa quadriluminis-Cyclosalpa polae* | 1.00 |
| *Cyclosalpa sewelli-Cyclosalpa polae* | 1.00 |
| *Iasis cylindrica-Cyclosalpa polae* | 1.00 |
| *Pegea confoederata-Cyclosalpa polae* | 1.00 |
| *Pegea sp.-Cyclosalpa polae* | 0.993 |
| *Ritteriella amboinensis-Cyclosalpa polae* | 1.00 |
| *Ritteriella sp.-Cyclosalpa polae* | 1.00 |
| *Salpa aspera-Cyclosalpa polae* | 1.00 |
| *Salpa fusiformis-Cyclosalpa polae* | 1.00 |
| *Salpa maxima-Cyclosalpa polae* | 1.00 |
| *Soestia zonaria-Cyclosalpa polae* | 1.00 |
| *Cyclosalpa sewelli-Cyclosalpa quadriluminis* | 0.999 |

| | |
|---|---|
| *Iasis cylindrica-Cyclosalpa quadriluminis* | 0.947 |
| *Pegea confoederata-Cyclosalpa quadriluminis* | 0.997 |
| *Pegea sp.-Cyclosalpa quadriluminis* | 1.00 |
| *Ritteriella amboinensis-Cyclosalpa quadriluminis* | 0.981 |
| *Ritteriella sp.-Cyclosalpa quadriluminis* | 1.00 |
| *Salpa aspera-Cyclosalpa quadriluminis* | 0.811 |
| *Salpa fusiformis-Cyclosalpa quadriluminis* | 0.820 |
| *Salpa maxima-Cyclosalpa quadriluminis* | 1.00 |
| *Soestia zonaria-Cyclosalpa quadriluminis* | 0.960 |
| *Iasis cylindrica-Cyclosalpa sewelli* | 0.993 |
| *Pegea confoederata-Cyclosalpa sewelli* | 1.00 |
| *Pegea sp.-Cyclosalpa sewelli* | 0.837 |
| *Ritteriella amboinensis-Cyclosalpa sewelli* | 1.00 |
| *Ritteriella sp.-Cyclosalpa sewelli* | 1.00 |
| *Salpa aspera-Cyclosalpa sewelli* | 0.889 |
| *Salpa fusiformis-Cyclosalpa sewelli* | 0.901 |
| *Salpa maxima-Cyclosalpa sewelli* | 1.00 |
| *Soestia zonaria-Cyclosalpa sewelli* | 0.999 |
| *Pegea confoederata-Iasis cylindrica* | 1.00 |
| *Pegea sp.-Iasis cylindrica* | 0.541 |
| *Ritteriella amboinensis-Iasis cylindrica* | 1.00 |
| *Ritteriella sp.-Iasis cylindrica* | 1.00 |
| *Salpa aspera-Iasis cylindrica* | 1.00 |
| *Salpa fusiformis-Iasis cylindrica* | 1.00 |
| *Salpa maxima-Iasis cylindrica* | 1.00 |
| *Soestia zonaria-Iasis cylindrica* | 1.00 |

| | |
|---|---|
| *Pegea sp.-Pegea confoederata* | 0.797 |
| *Ritteriella amboinensis-Pegea confoederata* | 1.00 |
| *Ritteriella sp.-Pegea confoederata* | 1.00 |
| *Salpa aspera-Pegea confoederata* | 0.992 |
| *Salpa fusiformis-Pegea confoederata* | 0.994 |
| *Salpa maxima-Pegea confoederata* | 1.00 |
| *Soestia zonaria-Pegea confoederata* | 1.00 |
| *Ritteriella amboinensis-Pegea sp.* | 0.674 |
| *Ritteriella sp.-Pegea sp.* | 0.923 |
| *Salpa aspera-Pegea sp.* | 0.356 |
| *Salpa fusiformis-Pegea sp.* | 0.364 |
| *Salpa maxima-Pegea sp.* | 0.997 |
| *Soestia zonaria-Pegea sp.* | 0.627 |
| *Ritteriella sp.-Ritteriella amboinensis* | 1.00 |
| *Salpa aspera-Ritteriella amboinensis* | 1.00 |
| *Salpa fusiformis-Ritteriella amboinensis* | 1.00 |
| *Salpa maxima-Ritteriella amboinensis* | 1.00 |
| *Soestia zonaria-Ritteriella amboinensis* | 1.00 |
| *Salpa aspera-Ritteriella sp.* | 1.00 |
| *Salpa fusiformis-Ritteriella sp.* | 1.00 |
| *Salpa maxima-Ritteriella sp.* | 1.00 |
| *Soestia zonaria-Ritteriella sp.* | 1.00 |
| *Salpa fusiformis-Salpa aspera* | 1.00 |
| *Salpa maxima-Salpa aspera* | 1.00 |
| *Soestia zonaria-Salpa aspera* | 1.00 |
| *Salpa maxima-Salpa fusiformis* | 1.00 |

| | |
|---|---|
| *Soestia zonaria-Salpa fusiformis* | 1.00 |
| *Soestia zonaria-Salpa maxima* | 1.00 |

Table 15: Tortuosity Comparisons Across Species

# Discussion

This study compared the swimming tortuosity and direction of salp colony chains across their colony architecture, species, and diel vertical migration behavior. We sampled 15 of the 48 described salp species and 5 of the 7 described colony architecture forms and observed that species known to vertically migrate from previous studies were more abundant at night in the subtropical open ocean and tended to have more linear, streamlined architectures. Salp swimming behavior varied across salp colony architectures and also varied depending on time of day. At night, vertically migrating species swam straighter and more downward than they did during the day. Collectively, our data support that streamlined colony architectures, straighter swimming paths and directional swimming may be advantageous for DVM.

## Day/Night Counts Indicate Differences in Migratory Behavior

Qualitative counts of each salp species in the daytime versus nighttime at our field sites provided evidence about which species migrate vertically and which do not, as salp migratory patterns have not been previously reported from our specific study regions (Kona, West Palm Beach, Panama). *Salpa* spp. and *Ritteriella* spp. were more abundant at night (Figure 3), consistent with their characterization as vertical migrators, which aligns with past work in the literature (Stone & Steinberg 2014, Madin et al. 1996). The species *Cyclosalpa sewelli*, *Pegea confoederata*, and *Brooksia rostrata* appeared with similar frequency during day and night, consistent with their characterization as non- migrators. Salp species previously identified as shallow migrators (*C. affinis* and *C. bakeri*) appeared slightly more frequently in the daytime than the night, which could potentially be because when they are migrating downwards during the day, they are still close enough to the surface to be recorded.

*Iasis cylindrica* is an interesting case because it dominated the other species in terms of frequency, and while it appeared more at night than in the day, it still appeared nearly as frequently during the day as non-migratory salp species. The literature categorizes *Iasis cylindrica* as being a migratory salp species (Stone & Steinberg 2014), however its high frequency in the daytime as well as the night indicates it is likely a shallow-migrating salp species as previously described (Madin et al. 1996).

Generally, the species of salps that migrate follow trends relating to salp colony architecture. Salps that are non-migrators (*Cyclosalpa sewelli* and *Pegea confoederata*) are cluster and transversal respectively, while the shallow migrating species *C. affinis* and *C. bakeri* are both whorl. Additionally, all deep migrating species are either linear (*Salpa* spp.) or bipinnate (*Ritteriella amboinensis*). The non-migrating bipinnate species *Brooksia rostrata* and the shallow migrating *Iasis cylindrica* are interesting exceptions to this pattern, indicating that colony architecture is associated with, but cannot always predict DVM behavior in a salp species.

**Tortuosity Indicates Straighter Swimming in Linear Chains and Deep Migrators**

Salps with linear colony architecture swam the straightest on average and swam significantly straighter than whorl salps, but not significantly different than the other architecture types (Figure 4). This result indicates that there is variance in swimming behavior between architectures to an extent, but not discretely between each architecture.

Overall, the swimming tortuosity across salp species was within range of other zooplankton. Salp swimming paths were similar to that of the krill *Thysaoessa raschii* (Price 1989), but salps swam straighter than the calanoid copepod *Temora longicornis* (Mouison et al. 2013), the water flea *Daphnia magna* (Toyota et al. 2022), and the ctenophore *Mnemiopsis leidyi* (Sutherland et al. 2014), though it is possible that these variances in swimming tortuosity could

be due to variables including the window of swimming time measured or environment (such as a lab versus open ocean).

Given that diel vertical migration (DVM) is a crucial part of the swimming behavior of many salp species, we expected that there would be differences in tortuosity between migratory salps and non-migrators, as well as between species that have different depth ranges of DVM. While migratory and non-migratory species did not have different tortuosity, deep migrators swam straighter than shallow migrators (Figure 5), including within the linear architecture group (Figure 6). This may be because salps that swim to greater depths during migration have to travel a greater vertical distance daily, which is energetically costly (Maas et al. 2018) resulting in a straighter path to minimize total swimming distance, while salps with a shallow DVM range do not travel as far and are thus less reliant on straight paths to conserve energy. For non-migrating salps, swimming in a tortuous pattern may be advantageous for accessing fresh patches of seawater and associated food particles while maintaining position near the surface where primary productivity is highest (Visser 2006).

Salps as a whole also swam straighter during videos taken in the nighttime compared to daytime (Figure 7). This is congruous with the evidence that salps with a deep DVM range swim straighter, as during the daytime the surface (where the *in-situ* video footage is taken) is dominated by primarily shallow migrating salp species as well as non-migrating salp species. During the nighttime, however, deep-diving salps make their way to the surface, where their presence causes the average swimming tortuosity to decrease. This pattern is reflected in the result that in daytime videos, there was no significant difference in tortuosity between non-migratory and migratory salp species (when the only migratory salp species present are shallow migrators) but in the nighttime videos, migratory salp species swam with significantly lower

tortuosity than non-migrators (when deep-migrating salp species are present at the surface) (Figure 8). Additionally, the greater abundance of migratory linear species at night may explain why linear architectures swam significantly straighter than transversal architectures in the nighttime, but not the daytime (Figure 9).

**Swimming Direction Suggests Vertical Swimming in Migrators**

Swimming direction did not vary across salp colony architectures (Figure 10) or diel vertical migration categories, possibly because sample sizes were small. However, cluster, linear and transversal architectures exhibited directional swimming with the average swim angle ranging from 94 to 108 degrees, indicating that salps are swimming mostly parallel to the surface or slightly downwards. Deep, shallow, and non-migrators also all had significant swimming directionality, so this directional swimming may be caused by behaviors other than DVM, such as avoidance of turbulence, which has been observed in cnidarian medusae that swim facing away from the coast to avoid waves (Malul et al. 2024) and ctenophores moving downward to avoid wind-driven turbulence (Jaspers et al. 2017).

The increased downwards swimming observed during the nighttime relative to the day (Figure 11) may relate to diel vertical migration behavior. Salps that exhibit DVM are generally known to stay in deep waters during the daytime and swim up to the surface at night (though reverse DVM also occurs (Pascual et al. 2017)), which appears to contradict the results of this study. However, one explanation for the trend of upward swimming seen in the daytime videos is that many of them were taken just before sunset, when light levels are decreasing and organisms may have been in the process of moving upwards towards the surface. Additionally, the observation of downward swimming during nighttime videos could be of migratory salps beginning to migrate back downwards, as most migratory zooplankton leave the surface about 20

minutes before sunrise (Bianchi & Mislan 2025). Alternatively, downward swimming could be a response to artificial lighting used during night videography, which may induce a downward swimming reaction as most zooplankton are negatively phototactic (Forward 1988). Overall, our results demonstrate a difference in swimming directionality among salps during different times of the day and these behaviors may relate to diel vertical migration. The results also show an association with salp colony architecture and swimming direction, as a majority of the downward swimming in the nighttime is done by linear colonies, while in the daytime a sizable amount of the upward swimming is done by whorl and cluster colonies (Figure 11).

**Ecological Implications**

We found that the architecture of a salp colony may influence swimming behavior, as the more streamlined architecture types such as linear swam straighter than the less streamlined architectures such as whorl. In addition to straighter swimming, past work found that linear colonies swim the fastest of the architecture types (Damian-Serrano et al. 2025). Linear colony architecture has also derived evolutionarily three separate times in salps (Damian-Serrano et al. 2023), indicating that a streamlined arrangement of zooids may be advantageous because of decreased drag when swimming through the water. Straighter swimming in zooplankton may also be associated with diel vertical migration behavior, as the migratory copepod *Centropages typicus* swam straighter when exposed to wavelengths of light that trigger DVM behavior (Cohen & Forward 2002). Given that many salp species with linear architecture are diel vertical migrators that are capable of a deep range (>50m) of migration in the water column (Weibe et al. 1979, Pascual et al. 2017), the streamlined colony architecture may be an adaptation that allows for more efficient migration. Overall, the connection between colony architecture and swimming

behavior may indicate that the diverse morphology of salp colonies may serve as adaptations to different lifestyles.

Conversely, the less-streamlined architectures (Cluster, Transversal, Whorl) had lower average tortuosity than Linear and Bipinnate, were more frequently seen in the daytime, and in previous work have been described as either not exhibiting DVM or having a small depth range; for example, the whorl salp *Cyclosalpa bakeri* only moves down to depths of 30-60m in the daytime (Purcell & Madin 1991). These salp species do not migrate as deep and therefore may not need to have a streamlined body plan that allows them to travel long distances in a short period of time. Instead, swimming may serve to reposition animals in new patches of seawater to enhance filtration.

Diel vertical migration is hypothesized to serve a variety of purposes: a primary one is to avoid visual predators such as fishes and seabirds by only surfacing at night; for crustacean larvae, this hypothesis has considerable evidence (Lampert 1989). However, for salps the predator avoidance hypothesis is more contested, as salp bodies are mostly transparent and difficult to see even in daylight (Purcell & Madin 1991). Another possible reason for diel vertical migration is to maximize feeding potential, such as by following prey that vertically migrate (Iwasa 1982). Some salps have DVM patterns that appear to maximize feeding as well as visual predator avoidance, as the deep-diving linear species *Salpa thompsoni* has been observed to start swimming upwards from deep water at midday, then spend a large amount of time in 30-120m of water where phytoplankton is rich, but far away enough from the surface to avoid predation from albatrosses, only surfacing in darkness (Nishikawa & Tsuda 2000). McLaren (1963) hypothesized that diel vertical migration may allow zooplankton to gain metabolic advantages from changes in water temperature at different depths. Purcell & Madin (1991) raise the point

that deep migrating salp species, such as *Salpa aspera* which can travel a vertical distance of 800m in the water column (Weibe et al. 1979), may benefit from traveling to colder temperatures at depth, which can slow the organism's metabolism to conserve energy.

While there is evidence that deep-migrating salp species' DVM behavior is associated with feeding, the shallow-migrating whorl species *Cyclosalpa bakeri* ceases its feeding when it is on the surface at night (Purcell & Madin 1991). DVM behavior of *C. bakeri* is hypothesized to be related to reproduction, as there is motile sperm in the testes of the salps in the night, when they are at the surface, but not in the day (Purcell & Madin 1991). Additionally, aggregating at the surface in groups is advantageous for reproduction as it maximizes successful fertilizations. However, to reproduce on the surface the salps must cease their feeding, as they are broadcast spawners and need to avoid sperm being caught in their mucus nets. It therefore appears that the function of DVM in salps may be species-specific, and shallow-migrating salps could be performing DVM behavior for a different purpose than deep-migrating species, which may also account for the differences in their swimming behavior. Future studies could investigate differences in behavior associated with DVM (feeding, metabolism, rate of predation) across different DVM depth ranges. Additionally, a more expansive study including more salp species across different latitudes and climates is necessary to develop a full understanding of the relationship between salp colony morphology and their behavior. Overall, this research develops our understanding of the connections between salp colony architecture and swimming behavior and offers implications about how colonial morphology may play a role in the way zooplankton adapt to different life strategies.

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