**Title: Colonial Architecture Modulates the Speed and Efficiency of Multi-Jet Swimming in Salp Colonies**

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**Running title:** Architecture Modulates Salp Swimming

**Summary Statement (30 words)**

Linear arrangements in multi-jet propelled marine colonial invertebrates are faster than less streamlined architectures without incurring in higher costs of transport, offering insights for bioinspired underwater vehicle design.

**Abstract**

Salps are marine pelagic tunicates with a complex life cycle including a solitary and colonial stage. Salp colonies are composed of asexually budded individuals that coordinate their swimming by multi-jet propulsion. Colonies develop into species-specific architectures with distinct zooid orientations. These distinct colonial architectures vary in how frontal area scales with the number of zooids in the colony. Here, we address how differences in frontal area drive differences in swimming speed and the relationship between swimming speed and cost of transport in salps. We (1) compare swimming speed across salp species and architectures, (2) evaluate how swimming speed scales with the number of zooids across colony in architectures, and (3) compare the metabolic cost of transport across species and how it scales with swimming speed. To measure swimming speeds, we recorded swimming salp colonies using in situ videography while SCUBA diving in the open ocean. To estimate the cost of transport, we measured the respiration rates of swimming and anesthetized salps collected in situ using jars equipped with non-invasive oxygen sensors. We found that linear colonies swim faster, which supports idea that their differential advantage in frontal area scales with an increasing number of zooids. We also found that higher swimming speeds predict lower costs of transport in salps. These findings underscore the importance of considering propeller arrangement to optimize speed and energy efficiency in bioinspired underwater vehicle design, leveraging lessons learned from the diverse natural laboratory provided by salp diversity.

**Keywords:** salps, colonial architecture, multi-jet propulsion, swimming, cost of transport

**Introduction**

Salps (Tunicata: Thaliacea: Salpida) are planktonic invertebrates that have a two-phase life cycle comprised of a solitary oozooid that asexually buds colonies of sexually reproducing blastozooids. Salp colonies are composed of up to hundreds of genetically identical, physically and neurophysiologically integrated pulsatile zooids (Bone et al. 1980, Mackie 1986). Zooids in the colony feed and propel themselves by drawing water in through the oral siphon, using muscle contraction to compress their pharyngeal chamber, and ejecting a jet of water from their atrial siphon (Bone & Trueman 1983). While solitary oozooids move using single-jet propulsion, salp blastozooid colonies integrate multiple propelling jets, which increases their thrust and reduces the drag that results from periodical acceleration and deceleration via asynchronous swimming (Sutherland & Weihs 2017).

Currently, there are 48 described species of salps (WoRMS, 2024) and while salps are widely distributed, most species are restricted to open ocean environments, far from the coast, which poses unique challenges to accessing them for direct study in their environment (Hamner et al 1975, Haddock 2004). Moreover, salps cannot be maintained alive in containers beyond a few hours since they are extremely fragile and sensitive to the presence of solid walls. Therefore, many morphological, ecological, and functional aspects of salp diversity, such as swimming speeds and metabolic demands, have remained unexplored. One such aspect is colonial architecture or the way that the zooids are arranged relative to each other in the colony. Salp colonies develop into species-specific architectures with distinct zooid orientations, including transversal, oblique, linear, helical, and bipinnate chains; as well as whorls, and clusters (Damian-Serrano & Sutherland, 2023). These architectures likely drive aspects of swimming performance (Madin 1990, Damian-Serrano et al. 2023).

In a multi-jet system, having a larger number of propellers can improve the hydrodynamic and inertial benefits granted by asynchronous multijet propulsion, in addition to providing additional thrust to the colony (Madin 1990, Sutherland & Weihs 2017). To our knowledge, the effect of varying numbers of propeller zooids on swimming speed has never been investigated in salps, nor how this relationship may vary across their diverse colonial architectures. Salp colonial architectures differ in how the number of zooids in the colony scales with their frontal area relative to motion (Madin 1990). Some architectures (linear, bipinnate, and helical) have a constant frontal area, regardless of zooid number. These architectures may benefit from increased thrust delivered by larger numbers of zooids while maintaining a constant frontal area and have been described as more efficient swimmers due to the reduction of drag associated with a more streamlined form (Bone & Trueman 1983). However, the rest of the architectures (oblique, transversal, whorl, and cluster) have an increasing (directly proportional) frontal area as the number of zooids increases (Fig. 1). Therefore, we expect the latter architectures to not only obtain more thrust, but to also experience more frontal water resistance as zooid number increases. As a result, we anticipate that swimming speed will be greater in colonies that bear a larger number of zooids, but only (or more so) for species with architectures that have a constant frontal area.

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Figure 1. Salp colonial architectures with representative species photos (*Pegea* sp. for transversal, *Cyclosalpa affinis* for whorl, *Cyclosalpa sewelli* for cluster, *Helicosalpa virgula* for helical, *Thalia cicar* for oblique, *Soestia zonaria* for linear, and *Ritteriella retracta* for bipinnate) and diagrams showing the distinct zooid orientations. The subsequent rows show the frontal view of colonies with four and eight zooids, with the final row indicating the expected frontal area increase factor between the four and the eight zooid colonies. In colonies with an expected frontal increase factor of 1 (helical, linear, bipinnate), frontal area stays constant as zooid number increases. Full black circles in the diagrams represent viscerae (guts) while the open circle represent siphons. Black straight lines inside the zooids indicate gill bars while gray straight lines represent endostyles.

The angle formed by the zooid axis and the colony axis (Fig. 2) could also influence swimming performance. This zooid-colony angle is determined by the degree of dorsoventral zooid rotation during development, which can span from 90°, in transversal chains with no rotation, to 0° (perfect linearity), in some linear chains such as those from the species *Soestia zonaria* (Damian-Serrano & Sutherland, 2023). While all blastozooid buds start their development in a transversal position, most species undergo this rotation largely during the first day of colonial development. Strong reductions in the dorsoventral zooid rotation angle toward linear forms have evolved multiple times independently (Damian-Serrano et al. 2023), possibly due to adaptive advantages related to their swimming efficiency.

Body size generally predicts swimming velocity in many animals (Andersen et al. 2016). However, colonial animals with multiple swimming units may circumvent this allometric constraint by having multiple propellers. Nonetheless, larger zooids might be expected to produce higher swimming speeds when comparing colonies with similar numbers of zooids.

Finally, pulsation rates (frequency that zooid ejects water from the posterior atrial siphon) may also influence swimming speed as has been shown in solitary salps (Madin 1990). Pulsation by salps serves the dual role of locomotion and filter feeding. The relationship between pulsation and speed might therefore be particularly relevant for species that undergo diel vertical migration (Madin et al. 1996) while in other species pulsation may serve to maximize filtration rates. Considering the tradeoffs between swimming and filtering, the eco-evolutionary relevance of swimming speed and the hydrodynamic efficiency likely varies between species (Damian-Serrano et al. 2023).

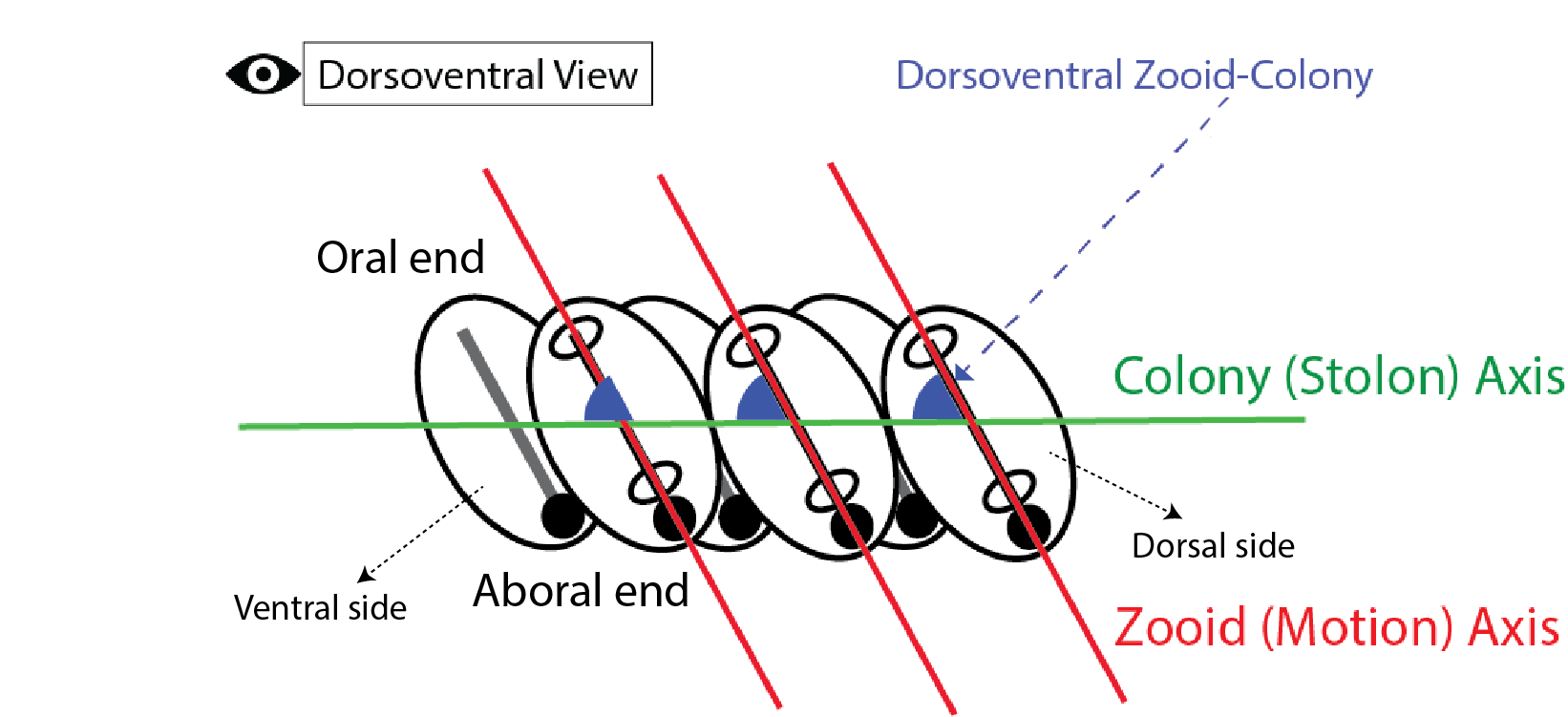


Figure 2. Schematic of an oblique chain from the dorsoventral perspective (dorsal for the top row, ventral for the bottom row) showing the zooid and colony axes and the zooid-colony angle, reduced by zooid rotation during colonial development. Black lines indicate gill bars (mostly occluded by the zooid axis) while gray lines represent endostyles.

The energetic costs of salp locomotion from mechanically estimated propulsive efficiency suggest that like other jet-propelled swimmers, salps are hydrodynamically efficient (Sutherland & Madin 2010, Gemmell et al. 2021, Trueman et al. 1984). The few metabolic measurements of swimming salps show that more active species-- in terms of swimming speed and pulsation rates-- have the highest respiration rates (Cetta et al. 1986) and that salps have higher respiration rates than other gelatinous taxa (Biggs 1977, Schneider 1992, Mayzaud et al. 2005, Trueblood 2019). However, the specific costs incurred by their swimming activity and their relationship to swimming speed have never been examined across the diversity of salp species.

In this study, we compare swimming speeds across 17 salp species and energetic costs of swimming across 15 species, encompassing all seven known salp colony architectures (Fig. 1, Table S1). In addition, we investigate how swimming speed varies with the number of propeller zooids and differences in frontal area scaling between colonial architectures. Finally, we compare cost of transport (COT) across salp species and assess how COT scales with swimming speed and pulsation effort.

**Materials and Methods**

*Fieldwork and videography* – We observed salps via 48 bluewater SCUBA dives (Haddock & Heine, 2005) from a small vessel off the coast of Kailua-Kona (Hawai’i Big Island, 19°42'38.7" N 156°06'15.8" W), over 2000 m of offshore water during September 2021, April 2022, September 2022 and May 2023. We spent a total of 42.2 hours (84.4 person hours: ADS & KRS) collecting and imaging salp colonies. Some dives were diurnal, where we collected most of the specimens of *Iasis cylindrica*, *Cyclosalpa affinis*, *Cyclosalpa sewelli*, and *Brooksia rostrata.* We observed and collected most specimens of other species during night dives (blackwater diving).

We recorded in situ underwater videos of salp colonies swimming using a variety of cameras including primarily a dark field stereovideography system (Sutherland et al. 2024), as well as a lightweight dual GoPro stereo system, a brightfield single-camera system (Colin et al. 2022), and a darkfield single-camera system. The primary stereovideography system was comprised of two synchronized high-resolution cameras (Z Cam E2, Nan Shan, Shenzhen, China and Sync Cable; 4K at 60 or 120 fps) with 17mm f/1.8 lenses (Olympus M.Zuiko Digital) housed in custom aluminum housings (Sexton Company, Salem, OR, USA). Each field of view was 23 x 42 mm and in-focus depth was 20-25 mm. The image from the right-hand camera was viewed using an external monitor (Aquatica Digital, Montreal, Quebec, Canada), and illumination was provided with two 10,000-lumen lights (Keldan, Bruegg, Switzerland). An L-shaped plastic framer helped the videographer position colonies in the field of view of both cameras. Before diving, the stereo system was calibrated in a swimming pool using a cube with reflective landmarks. Calibration images were processed using the CAL software package (SeaGIS measurement science, Bacchus Marsh, Victoria, Australia). Over the course of the study, we observed 241 salp colonies (N) from 18 species and recorded 1,946 measurements (n) (Dataset1A, Table S1). Throughout the manuscript, we refer to the number of specimens as N and the number of measurements as n.

*Measuring salp colony swimming speed* – For most species, we collected and analyzed footage from multiple specimens (Dataset1A, Table S1). We analyzed the swimming behavior of salp colonies arranged in linear (six species, 64 specimens), bipinnate (three species, 17 specimens), whorl (three species, 10 specimens), cluster (two species, eight specimens), and transversal (one species, two specimens) architectures, with oblique and helical architectures represented by a single specimen. We used a combination of spatially calibrated stereo video and 2D videos with a reference scale in the frame. Increments on the scale ruler were 1 mm and we estimate that measurements made in ImageJ are accurate to the tenths place. From the stereo videos, we manually selected and measured the relative XYZ positions of salp colony zooids in EventMeasure (SeaGIS). We implemented a cutoff in the RMS (root mean squared) point error estimate of < 2 mm.

We complemented gaps in taxon sampling with archived 2D videos in the lab from previous expeditions to West Palm Beach (FL, USA) and the Pacific coast of Panama. These two-dimensional single-camera videos were collected using a Sony FDR-AX700 4K Camcorder (3840x2160 pixels, 60-120 fps) with a Gates Underwater Housing (Poway, CA, USA) using brightfield illumination (Colin et al 2022) or darkfield illumination. For these 2D videos, we used the FFMPEG plugin in ImageJ to manually select and measure the relative XY positions of salp zooids in sequences where the colony was swimming horizontally within the focal plane. The colonies were assumed to be in the same plane as the scale bar so at same distance from the camera. However, in videos with a broad focal depth, this may not always had been the case, thus potentially introducing some measurement error.

We tracked and manually selected the position of the first zooid’s viscera (using a contrast-based centering macro to mark the center point) as well as the position of a reference particle in the water (methods described in Sutherland et al. 2024) in 10-30 frames across 50-500 frame windows spanning 2-4s of swimming on the synchronized left and right videos in EventMeasure. The reference particle was a non-swimming organism (such as a foraminiferan or radiolarian) or a non-living particle. For each analyzed frame, we calculated the horizontal x, vertical y, and depth z (in the case of the stereo video measurement files) positions of the frontal zooid relative to the reference particle.

We then calculated the instantaneous relative speeds of the frontal zooid using Eq. 1 (without the z component in the case of the 2D videos), where t refers to instantaneous time points. Time points were extracted from the frame rate of the video and the spacing between frames chosen for analysis. Our videos presented variability in frame rate with a minimum of 28, 1st quartile of 60, median of 120, 3rd quartile of 97, and a maximum of 240 frames per second. Moreover, the temporal spacing between measurements varied between videos with minimum of 0.07s, a 1st quartile of 0.16s, a median of 0.17s, a 3rd quartile of 0.25s, and a maximum = 0.5s.

Eq. 1

In addition, we recorded the pulsation rates of the specimens measured by counting the number of times the atrial siphon contracted in a known period.

*Salp colonial architecture* – To examine the relationships between locomotory variables and colonial architecture, we adopted the species-specific architecture characterizations and zooid-colony angle measurements for each species from Damian-Serrano et al. (2023). Using stills from the underwater videos, we measured zooid length, zooid width, and number of zooids in ImageJ by manually selecting the point coordinates. These measurements were repeated in at least three locations from each colony. When a distinct zooid size gradient was observed, we measured zooids in locations from the proximal, middle, and distal regions to capture the full range of variation in the specimen. The scale ruler in images had 1 mm increments and we estimate an accuracy to 0.1 mm based on the pixel resolution of the images (minimum resolution=1440x1080 pixels; maximum resolution: 3840 x 2160).

*Respiration measurements* – We collected healthy, adult blastozooid (aggregate stage) colonies across 18 salp species (Dataset S1B) during blue- and black-water SCUBA dives off the coast of Kailua-Kona (Hawaii, USA) between September 2021 and May 2023. We analyzed the respiration rates of salp colonies arranged in linear (seven species, N = 46), bipinnate (three species, N = 29), whorl (three species, N = 23), cluster (two species, N = 18), and transversal (one species, N = 13) architectures, oblique chains (*Thalia* sp., N = 7), and helical architectures represented by *Helicosalpa virgula* (N = 2). Specimens were sealed *in situ* with their surrounding water in plastic jars equipped with a PreSens oxygen sensor spot (Regensburg,Germany) and a self-healing rubber port to allow for the injection of solutions without the introduction of air bubbles. We removed as many symbiotic animals from the salps as possible before closing the lid without damaging the colony. The same method was applied to one or more seawater controls to account for the oxygen demand of the local seawater’s microbiome. Several collection events occurred during each 20-60 min long SCUBA dive. Jars with larger animals were opened during the safety stop to allow them to re-oxygenate. Upon the divers' return to the boat, we measured the initial oxygen concentration (mg/l) and temperature and then repeated the measurements at intervals between 15min and 3h, for total periods ranging between 2h and 5h, depending on logistic constraints in the field and the rate of oxygen depletion. The exact interval time for each measurement was variable but recorded (Dataset S1B, mean time interval spacing = 11.1 min, standard deviation = 14.6 min, median = 7.3 min).

To estimate the energetic expenditure of different salp species while actively swimming, we recorded the oxygen consumption of intact specimens while swimming inside the jar. To obtain a baseline of basal respiration rate (while not swimming), we anesthetized some specimens before the start of the first oxygen measurement time. A few specimens were used for paired experiments, where their swimming respiration was recorded for a few hours, then inoculated with the anesthetic, and recorded anesthetized for another set of hours. To anesthetize salps, we injected their jars with small volumes of concentrated (50 g/l) bicarbonate-buffered MS-222 through the rubber ports on the lids. We tailored the injection volume to the jar size aiming for a final concentration of 0.2g/l, following the methods in Trueman et al. (1984). We also injected some seawater control jars to evaluate the effect of MS-222 on oxygen concentration in seawater and found no effect.

When multiple seawater controls were collected using jars of different sizes, we paired each jar with the control that had the most similar volume. If among multiple controls only some were jars injected with anesthetic, we paired the anesthetized specimen jars with the injected controls and the intact specimen jars with the intact controls. In experiment 26 (see Dataset S1B for experiment numbers), the control jar was lost due to an encounter with an oceanic white tip shark, thus we paired those measurements with the nearest relative time points from the control jar in experiment 25, collected the same day hours earlier. At the end of each experiment, we identified the salp specimens used in the experiments to the species level, counted the number of zooids, measured the zooid length (total length including projections), and measured the biovolume of the colony using a graduated cylinder. For those specimens where colony or zooid volume was not measured directly, we estimated the colony volume from their zooid length and the number of zooids using a Generalized Additive Model with the measured specimens.

We estimated the mean oxygen consumption rate for each specimen by fitting a linear regression of consumed oxygen mass (concentration by container volume) against the duration of the measurement series. We subtracted the slope calculated for the relevant control jar to the estimated slope of the animal jar. Since our seawater controls were not filtered, some experiments had abnormally high estimated background respiration rates, leading to negative values. We removed these data points before the analysis. To estimate biovolume-specific rates, we divided the rates by the colony volumes. We then compared the biovolume-specific respiration rates of active (swimming) and anesthetized specimens within each species, calculating the difference as a measure of biovolume-specific swimming cost respiration rate. Biovolume was used instead of dry mass to normalize measurements due to the inherent difficulties of accurately measuring dry mass of these fragile gelatinous organisms in the field. Biovolume provides a consistent and reliable measure of the live size of the colony, which is directly relevant to the volume of water being displaced during swimming. We also calculated the relative investment in swimming as the proportion of biovolume-specific respiration rate comprised by the swimming-specific rate. To capture variability within species, we calculated the mean respiration rate of anesthetized specimens for each species and subtracted it from each intact specimen’s total respiration rate to get multiple swimming-specific rate values within each species. Some species had higher average respiration rates among the anesthetized specimens than among the swimming specimens, leading to negative swimming-specific respiration estimates. We interpreted this anomaly as a systematic error due to the extremely low respiration rates of some species that fall within the effective detection limit of our experimental setup given the random variation range of respiration rates in seawater both in experimental jars and in control jars. Small absolute negative values get amplified into large relative values, especially in small animals with a minuscule biovolume denominator. Therefore, we removed the swimming specimens that had lower respiration rates than the mean anesthetized respiration rate for their species. We also removed two respirometry outliers of *Thalia* sp. which had extremely high swimming respiration rates (>7500 pgO2/ml/min, whereas all other measurements across species including other *Thalia* sp. were limited to 0-1700 pgO2/ml/min), which were likely due to amplification of experimental error (presence of organic matter or symbionts, underestimation of colony volume due to loss of tiny zooids in the sieves) with the small biovolume denominators in this species.

*Estimating costs of transport* – We define the cost of transport (COT) as the amount of oxygen consumed per tissue volume per distance traveled by the colony. To estimate the COT, we divided the swimming-specific respiration rates by the mean swimming speed for each species measured from the stereo and 2D video data. Since the specimens used for speed measurements in the videos and those used in the respirometry experiments had different zooid sizes, we used the mean zooid-lengths per second speeds from the video measurements and then multiplied them by the actual zooid lengths of the respirometry specimens to estimate their absolute (mm/s) speeds. Pulsation rate estimates were taken from species averages from the video specimens. We also calculated the size-specific COT by transforming the swimming distances into zooid lengths measured from the respirometry specimens.

*Statistical Analyses* – All data wrangling and statistics were carried out in R 3.6.3 (R Core Team 2021). Before each quantitative statistical analysis, we compared an array of linear mixed random-and-fixed effects models, where the main predictors were coded as fixed effects. One of the models would have only the fixed effects, while another would also incorporate the random effects of the specimen and/or those of the species to control for pseudoreplication. The random effects term of the mixed model where both species and specimen terms were included had specimen coded as a nested term within species. We then used Akaike’s Information Criterion (AIC) to identify the best fitting model. When two or more models had a delta within 2 units, they were considered to have a comparable goodness-of-fit. In such cases, the simplest model with least number of parameters was chosen. We will refer to the model with only the primary predictors’ fixed effects as the “fixed-effects model”, to the mixed model that also includes species random effects the “species model”, to the mixed model with specimen random effects as the “specimen model”, and to the mixed model that contains the nested random effects of species and specimen as the “mixed model”. To test for differences between architectures, we used linear mixed models with Tukey’s post-hoc pairwise contrasts calculated using estimated marginal means, reporting the difference magnitude and the p-value in supplementary tables S2A and S2B. We tested the significance of the effect of architecture by comparing the mixed model to a null model without the fixed effects of architecture using an ANOVA. To test the relationships between pairs of continuous variables across architectures (e.g. swimming speed vs. number of zooids), we used linear mixed model regressions. We evaluated the significance of the slope parameter when compared against a flat slope (one-tailed t-test) to test whether changes in the independent variable (e.g. number of zooids) were associated with changes in the dependent variable (e.g. swimming speed). Owing to the patchiness of some species despite 80+ hours spent underwater (Table S1), we used replicate measurements (n) from each specimen (N) in swimming speed mixed models and regressions. We used an exponential regression to test the relationship between speed and COT. Specimen means (N) were used for all COT comparisons and regressions. Individual measurements (n) were used up to determine oxygen consumption rates. To evaluate the relative contribution of zooid size, pulsation rate, zooid number, and architecture type on swimming speed, we fitted a linear mixed model and evaluated the significance and proportion of variance explained by each factor using their marginal R2. To abbreviate, we will report conditional R2 as cR2, marginal R2 as mR2, and degrees of freedom as df.

**Results**

Salp colony swimming speeds, pulsation rates, and respiration rates varied within and across species and colony architectures. When considering speed in terms of mm/s, AIC testing selected the mixed model, which found no relationship between pulsation rate (effort) and absolute speed (n = 947, N = 111, 18 species, Speed mm/s = -0.1\*Pulsation rate + 47.4, cR2 0.88, mR2 = 0.00, p = 0.97, df = 128.2, Fig. S1A), nor with zooid-size corrected swimming speed, for which AIC testing also selected the mixed model (n = 848, N = 100, 18 species, Speed zooid lengths/s = 0.1\*Pulsation rate + 2.9, cR2 0.83, mR2 = 0.002, p = 0.64, df = 131.6, Fig. S1B). Normalized swimming speeds (zooid lengths per pulse) allow for a more direct comparison of swimming speed across colonial architectures.

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Figure 3. Boxplots showing the absolute (A) and corrected for body size and pulsation rate (B) swimming speeds recorded for each salp species and architecture (C, D) respectively. Colors correspond to colonial architecture types. Sample sizes are included in the legend and Tukey’s post-hoc pairwise comparisons across architecture types are listed in Dataset 1A and Table S2A, respectively.

*Swimming speeds across salp architectures*

Our model selection via AIC favored the mixed model when modeling the effects of absolute swimming speed as well as when modeling the effects of relative speed in zooid-lengths per pulsation. Absolute swimming speed varied significantly (5 architectures, 16 species, N = 109, n = 913, cR2 = 0.88, mR2 = 0.42, ANOVA vs. null model p = 0.0009, Fig. 3C) between colonial architecture types, and so did relative speed (cR2 = 0.78, mR2 = 0.14, ANOVA vs. null model p = 0.019, Fig. 3D, Table S2A). Speeds measured with 2D methods were slightly slower than those measured with 3D methods within the species in which they overlapped. This is to be expected since 2D methods cannot account for the z (depth) component of the speed vector. Measurements of helical and oblique chains were limited to a single specimen, so they were excluded from the analysis. In terms of absolute speed (mm/s), linear architectures were significantly faster than every other architecture (Tukey’s p < 0.05) except clusters. No other differences were significant. In terms of relative speed (zooid lengths/pulse), Tukey post-hoc tests did not reveal any significant differences between architectures.

Since linear architectures had the fastest mean swimming speeds (Fig. 3C, D), we investigated the relationship between swimming speeds with the dorsoventral zooid-colony angle (Fig. 4). For both absolute and relative swimming speed, AIC favored the mixed model. Species with lower zooid-colony angles presented faster absolute speeds (n = 910, N = 107, 16 species, Speed mm/s = -0.8\*DV Zooid-Colony angle + 84.4, cR2 = 0.87, mR2 = 0.29 p = 0.0014, df = 14.7) and faster size-and-effort corrected swimming speeds (n = 810, N = 96, 16 species, Speed zooids/pulse = -0.02\*DV Zooid-Colony angle + 2.4, cR2 = 0.77, mR2 = 0.10 p = 0.019, df = 14.5).

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Figure 4. Absolute (A) and relative (B) colony swimming speed (specimen mean with standard errors, total n=103) for each salp species across their dorsoventral zooid-colony angle. Error bars indicate standard error. The color indicates colonial architecture. Gray areas indicate the 95% confidence interval of the linear regression (black line).

We compared how swimming speeds scale with the number of zooids in the colony and found differences between colonial architectures. Relative swimming speed in whorls increased with number of zooids (n = 84, N = 10, 3 species, Swimming speed zooids/pulse = 0.1\*Number of zooids + 0.1, cR2 = 0.75, mR2 = 0.34, p = 0.025, df = 7.99) according to the AIC-selected specimen model, though the data for this architecture was limited to small numbers of zooids (4 to 13) and relatively slow speeds (under 51.0 mm/s). Linear chain architectures did increase in relative speed with the number of zooids (n = 443, N = 52, 6 species, Swimming speed zooids/pulse = 0.02\*Number of zooids + 2.0, cR2 = 0.45, mR2 = 0.11, p < 0.0001, df = 439.2) according to the AIC-selected species model. This relationship was not significant for any of the other architectures (clusters assessed with a specimen model, transversal chains assessed with a fixed model, and bipinnate chains assessed with a specimen model).

We pooled the data from multiple architectures into scaling modes to evaluate the overall relationship in colonies with a constant frontal area (linear, bipinnate, and helical species) and in colonies with scaling frontal area (transversal, whorl, cluster, and oblique species) with linear regressions (Fig. 1). This aggregation allowed the inclusion of data from architectures for which we only had one specimen (helical and oblique). When pooled by scaling mode (Fig. 5), the AIC-selected mixed model on colonies with a constant frontal area had a higher intercept on the relative swimming speed axis than the specimen model (equal AIC support to the mixed model but simpler) in those with a scaling frontal area (1.7 and 1.0 zooid lengths/pulse, respectively), reflecting the generally higher swimming speed of colonies with constant frontal area. Moreover, the mixed model regression on colonies with constant frontal area had a significant positive slope (n = 607, N = 71, 10 species, Speed zooids/pulse = 0.02\*Number of zooids + 1.7, cR2 = 0.80, mR2 = 0.072, p = 0.062, df = 72.6), while the specimen model regression on those with scaling frontal area was not significant (n = 241, N = 29, 8 species, p = 0.36, df = 243.9). The limited sample sizes for helical and oblique chains prevent us from drawing firm conclusions about these architectures.

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Figure 5. Linear relationships between relative swimming speed (zooid lengths per pulsation, specimen mean with standard errors) and number of zooids in the colony. (A) shows species with constant frontal area (N = 71). (B) shows species with a frontal area that is expected to scale with the number of zooids in the colony (N=29). Gray areas represent the 95% confidence intervals of the regressions.

Putting together all the different organismal factors that we analyzed in this study, AIC comparisons favored a mixed model to predict absolute salp swimming speed (U) from the fixed effects of zooid length (L), pulsation rate (P), number of zooids (Z), colonial architecture represented as frontal area scaling mode (A), as well as the random effects of nested species grouping (S) and specimen grouping (N) as expressed in Eq. 2.

Eq. 2

In this global model, we found significant effects on swimming speed (848 measurements, 100 videos, 18 species, U = 0.3L – 0.3P – 0.1Z – 48.8A + 63.1, cR2 = 0.86, mR2 = 0.34) only for A. We found that our fixed-effects predictors explain 34% of the variance in our swimming speed data: 2.7% is explained by zooid size (not significant), 0.03% by pulsation rate (not significant), 0.00% from zooid number (not significant), and 32% by the frontal scaling mode (p = 0.00047).

*Respiration rates and cost of transport (COT)*

The respiration rates of swimming and anesthetized salps revealed broad differences between species (Fig. 6, S2A). After estimating the absolute COT, we found a few significant differences between architectures using a species model (AIC favored specimen and species models equally; mR2 = 0.52, Fig. 6C, ANOVA vs. a null model p < 0.0001, Table S2B). In terms of absolute COT traveled, all architectures except oblique chains had similar high transport efficiencies under 13 pgO2/ml. Every one of these architectures was significantly more efficient per mm traveled than oblique architectures (Tukey’s p < 0.02). No other differences were found to be significant. In terms of relative COT (normalized to zooid length traveled), AIC favored a species model (mR2 = 0.29, Fig. 6D, ANOVA vs. a null model p = 0.0096, Table S2B). Post-hoc testing of this model showed no significant differences between architectures. Some of the differences between COT per mm and COT per zooid length are likely due to scaling with body size, as can be observed with the relative shift in the minuscule *Thalia* sp. (5.2 mm zooids) and the massive *Salpa maxima* (93.4 mm zooids).

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Figure 6. Mean cost-of-transport per mm (A) and per zooid length (B) moved for each salp species, and for each colonial architecture (C, D) with standard errors. Bar colors indicate colonial architecture. Sample sizes and Tukey’s post-hoc pairwise comparisons across architecture types are listed in Dataset 1B and Table S2B, respectively.

When comparing the proportion of investment of metabolic costs into swimming (compared to the species mean baseline) across salp species (Fig. S2B), eight species had locomotion budgets under 50%, and the other seven have budgets above 50%. We then compared the proportion of energetic investment in swimming to the COT values across species (Fig. S3A,B). The AIC-selected species model showed a significant relationship with absolute COT (N = 74, 14 species, Swimming % = 0.6\*COT per zooid length + 45.0, cR2 = 0.54, mR2 = 0.11, p = 0.0023, df = 77). Another AIC-selected species model also found a positive relationship with zooid-length scaled COT (N = 74, 14 species, Swimming % = 0.2\*COT per zooid length + 36.2, cR2 = 0.78, mR2 = 0.34, p < 0.00001), indicating that species with more costly locomotion per zooid length invest a larger proportion of their energy budget in swimming. Finally, we compared the proportion of energetic investment in swimming with speed (Fig. S3C,D). We found no relationship (neither in mm/s nor in zooids/s, both analyzed with the favored species model), indicating that faster swimmers do not invest more of their energy budget into their locomotion efforts. We found that regardless of whether we consider transport in terms of absolute distances (Fig. 7A, N = 64, 14 species, linear model: COT per mm = -0.1\*Speed mm/s + 12.8, cR2 = 0.48, mR2 = 0.064, p = 0.067, df = 43.4; exponential model: logCOT per mm = -0.02\*Speed mm/s + 1.6, cR2 = 0.47, mR2 = 0.15, p = 0.0043) or relative to body lengths (Fig. 7B, 64 specimens, 14 species, linear model COT per zooid length = -13.9\*Speed zooid lengths/s + 119.2, cR2 = 0.32, mR2 = 0.095, p = 0.095; exponential fixed model (equal AIC support to the species model) logCOT per zooid length = -0.2\*Speed zooid lengths/s + 4.3, adjusted R2 = 0.14 p < 0.001), the COT decreases in species with faster swimming speeds, but these relationships are only significant when fitting an exponential model with logCOT.

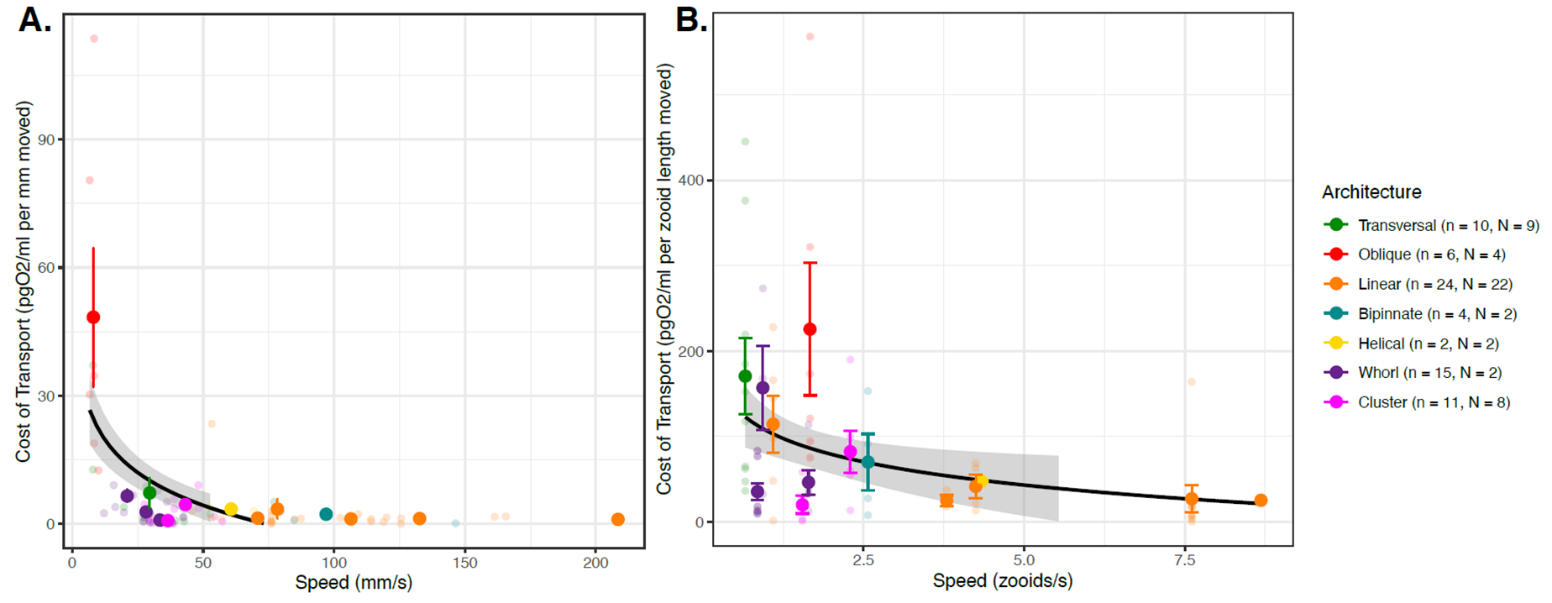


Figure 7. COT (specimen mean with standard error, n=75) per mm (A) and zooid length (B) moved across the specimen mean absolute (A) or relative (B) swimming speeds. The dot color indicates colonial architecture. Gray areas represent the 95% confidence intervals of the exponential regressions (black lines).

**Discussion**

We compared the swimming speeds and costs of transport of salp colonies across a comprehensive representation of salp species diversity. Our results show a wide range of colonial swimming speeds across salp species and architectures, where species presenting a linear colonial architecture had the fastest swimming speed (Fig. 3). Moreover, this study shows for the first time how salp colonial swimming speed scales with the number of zooids in the colony (Fig. 5), suggesting that incremental propulsive power from additional zooids does produce higher swimming speeds for species with a constant frontal area. Across species, salps have a low COT (Fig. 6) and as speed increases, COT decreases (Fig. 7), which may be a unique advantage of multi-jet swimmers.

*Architectural determinants of salp swimming speed*

Colonial architecture was the strongest predictor of swimming speed, though there is a large amount of unexplained variation which may relate to species-specific differences, behavioral, or environmental factors (see global mixed model results). We expected that swimming speed in colonial salps would be predicted by pulsation rate as a measure of swimming effort (Fig. S1). Our results indicate that this relationship is not significant, suggesting that salp swimming speed is driven by other factors. We did find a significant increase in pulsation-corrected speed with larger zooid sizes (Fig. S1D), consistent with previous findings of jet-propelled invertebrates (Gemmell et al 2021; Bone and Trueman 1983) and more broadly across aquatic swimmers (Andersen et al. 2016). An underlying relationship between pulsation rate and zooid length may be mask the relationship between pulsation rate and absolute speeds. This is consistent with the distribution of our data and our observations in the field where larger salps pulsate at a slower rate than smaller ones.

The relationship between the number of zooids and speed in linear chains is complicated by shifts in zooid orientation during development. Salp colonies start their free-living phase when the developing buds detach from the solitary oozooid. The newly released colony has the maximum number of zooids since the zooid number only gets reduced as the colony splits or loses zooids to turbulence, disease, or predation. Therefore, colonies with higher numbers of zooids are typically composed of smaller, younger zooids. In linear architectures, these younger colonies could still be developing their dorsoventral rotation (Damian-Serrano & Sutherland 2023), thus effectively being more like oblique architecture. A less acute dorsoventral zooid-colony angle would explain why these more numerous linear chains are not as fast as we would expect, given that our results support a significant relationship between zooid-colony angle and swimming speed (Fig. 4). Finding a strong relationship between zooid number and speed in whorls was surprising given their less streamlined configuration (Fig. 5). This could be due to the smaller range of slow speeds and few zooids in the data we obtained for these species. Our regression results on pooled architectures, as well as finding a significant relationship between number of zooids and speed for linear chains but not for clusters nor transversal chains, support our primary hypothesis that the different frontal area scaling relationships across architectures has an impact on swimming speed. However, we did not find support for such relationship in bipinnate chains, which also present a constant frontal area. This may be due to similar developmental bias as in linear chains, where younger colonies are not fully developed in their architecture and experience a more viscous Reynolds regime with their smaller body sizes.

Linear chains swam faster than all other architectures, including those that share a constant frontal area feature like bipinnate chains (Fig. 3, Table S2). One potential explanation for this difference could come from the relative thrust provided by the jets. Linear chains eject their jet plumes at very small angles (near parallel) to the axis of locomotion (Sutherland et al. 2024), just wide enough to avoid interaction between jet plumes (Sutherland & Weihs 2017). Bipinnate and helical chains (both with constant frontal area) have the atrial siphons (point of jet ejection) of their constituent blastozooids oriented at a wider angle (Madin 1990), which may lead to wider angles of their jets relative to the axis of locomotion. This in turn would result in a larger proportion of the force exerted by the jet to be applied as torque rather than thrust onto the colony. This hypothesis could be tested by measuring the 3D angles of the actual jets instead of the angles of the zooids since salps can use their atrial muscles and siphon morphology to direct the angle of their jets.

Finding that clusters can swim at speeds comparable to those of bipinnate and helical chains, even faster than whorls, defies our intuitive understanding of the mechanical properties of these colonies and thus warrants further investigation. While oblique chains are architectural intermediates between transversal and linear chains (Damian-Serrano & Sutherland 2023), our data indicate that oblique chains may be the slowest swimmers among salps. This incongruence may be explained by the fact that we only had speed data from one oblique specimen (of *Thalia* sp.) with very small zooid sizes. Small salps operate at lower Reynolds numbers than large ones, which may require a non-linear size correction for meaningful speed comparisons. Swimming speed data from the much larger oblique chains of *Thetys vagina* may provide a more comparable example of the locomotory performance of this oblique colonial configuration.

The questions addressed in this study focus on the effect of frontal area of colonial architectures on swimming speed. This effect may be associated with form and pressure drag differences between more and less streamlined colony shapes. To test whether these are the forces responsible for differences in swimming speed, drag would have to be measured or calculated, which is beyond the scope of this study. Other unaccounted forces may be significant energetic contributors to the system that explain the remainder of the observed variation. Chain length for the streamlined forms (helical, linear, and bipinnate chains) could have negative effects on swimming speeds that may partially counteract the positive effect of increased propeller thrust. For example, skin drag increases proportionally to the surface area of the system, and the smoothness of the chain may increase pressure drag through vortex shredding (Vogel 1981). While added (virtual) mass could also be an issue, asynchronously swimming colonies do not suffer as much from these acceleration-related costs, since their speed is maintained near constant while cruising (Bone & Trueman 1983). Chain length could also lead to reduced stability and efficiency, though some species with linear architectures capitalize on this by swimming in corkscrew orbital spirals (Sutherland et al. 2024). However, if friction drag, chain stability, or vortex shredding were indeed more important contributors than frontal form drag, we would predict that linear chains would appear slower than other more stable and compact architectures. Future studies may unravel these potential confounding effects on the biomechanics of colonial salp swimming.

*Salp swimming speed and diel vertical migration*

Salps are important players in the oceanic carbon cycle, grazing upon both phytoplankton and bacteria (Henschke et al. 2016). Their carcasses and fecal pellets export large quantities of fixed carbon into the deep sea, accelerating carbon sequestration in the biological carbon pump (Wiebe et al. 1979, Décima et al. 2023). Part of this process is enhanced by the diel vertical migrations by some salp species though the distribution of this behavior across species diversity is poorly known. Off Bermuda, Madin et al. (1996) reported *Pegea* spp., *B. rostrata*, and *C. polae* as non-migratory, all of which we found to have slow swimming speeds. Other slow-swimmer species like *C. affinis* were found to only migrate a few meters through the diel cycle. The species *S. aspera, S. fusiformis*, *S. zonaria, I. punctata,* and *R. retracta* have been observed vertically migrating off Bermuda (Madin et al 1996, Stone & Steinberg 2014), which is congruent with our observations during fieldwork. These species all have constant frontal area and fast swimming speeds.

Vertical migrators need to be fast enough to follow the dark isolumes as they shift during dawn and dusk in time to maximize their exploitation of the food resources near the surface. Thus, absolute speed is important to the ecology of these animals. Other *Salpa* species have also been reported as strong vertical migrators throughout the literature (Henschke et al. 2021, Madin et al. 2006, Pascual et al. 2017). A species that does not fit this pattern is *I. cylindrica*, a fast-swimming non-migratory species that spends night and day near the surface (Madin et al 1996; and pers. obs.). However, other studies do report moderate diel vertical migration for this species (Stone & Steinberg 2014), so it may be adapted for facultative vertical migration under specific oceanographic conditions. Some migratory species, such as *S. aspera*, are known to travel distances of over 800m at dawn and dusk, at rates predicted to require 5-10 m/min (83-166 mm/s) based on MOCNESS trawl intervals (Wiebe et al. 1979). These predictions are consistent with the speeds we recorded for this species (88-145 mm/s) and similar congenerics.

*Ecophysiological implications*

A few well-studied vertically migrating salp species are known to play a role in the biological carbon pump (Décima et al., 2023), the process by which biological activity (such as the feeding and defecation of salps) in the ocean’s water column transports carbon from the atmosphere into deep water. The question of whether this ecological role is generalizable to other salp species remains unanswered. In addition to vertical migration behavior, another likely important factor in their carbon flow is their respiration rate. The higher their respiration rate, the larger the proportion of assimilated carbon that will be released back into the water as dissolved carbon dioxide. This study provides the broadest taxonomic perspective on respiration rates (18 species, Fig. S2A) and swimming cost of transport (14 species), finding 17-fold differences in their respiration rates and over 77-fold differences in their mean COT. Except for a few species with extremely high and low values, most respiration rates are centered between 0.2 and 1 µmol/g/hour, assuming a salp tissue density of 1.025 g/ml. In general, the respiration rates we estimated for salps are within the range of those reported in the literature (Trueblood 2019, Iguchi and Ikeda 2004). Compared to the metabolic rates estimated for the broader diversity of marine pelagic animals (Seibel & Drazen 2007), the rates that we measured for salps are in a similar range to those measured for *Salpa thompsoni* (Iguchi and Ikeda 2004). Our values are also similar to those measured by Seibel & Drazen (2007) in nemerteans, chaetognaths, and most fishes (0.1-1 µmolO2/g/h), which are generally higher than other gelatinous animals like ctenophores or scyphomedusae (0.01-0.1 µmolO2/g/h), but generally lower than those of cephalopods, crustaceans, or large fish (1-10 µmolO2/g/h). Salp species known to have strong vertical migration behaviors (*Salpa* spp., *S. zonaria, I. punctata,* and *R. retracta)* have low basal metabolic rates (Fig. S2A) and low costs of transport. These results indicate that many non-migratory species, while likely still being important players in the biological carbon pump via their fecal pellet production, are releasing more of the consumed carbon as carbon dioxide near the surface than their more metabolically efficient relatives. The ultimate ecological outcome of each species needs to be assessed holistically, considering their microbial filtration and pellet deposition rate as well as their relative abundance in the water column.

Our metabolically calculated costs of transport range between 5-50 J/kg/m when converting the mg of oxygen to J via aerobic respiration free energy equations at 23°C. These values are higher than the highly efficient 1-2 J/kg/m reported for salps in the literature (Bone & Trueman 1983, Gemmell et al. 2021), and approach the less-efficient values found in single jet-propelled invertebrates like scallops or squids. We suspect that COT calculated from mechanical parameters such as the displacement of water mass is not directly comparable to the COT calculated from respiration rates. Furthermore, the standard aerobic respiration free-energy equation based on glucose may not fully represent the metabolic energy-conversion processes in salps, which could rely on a combination of sugars and fatty acids derived from their microscopic prey.

While COT increases with swimming speed in fishes (Rubio-Gracia et al. 2020) and jet-propelled squid (Bi & Zhu 2019), multi-jet swimmers may circumvent this tradeoff by having multiple swimming units. In colonial siphonophores, as zooid number increases swimming speed increases together with a decrease in COT (Du Clos et al. 2022). Our results show that faster swimming species have exponentially lower COT (Fig. 6), which suggests that faster speeds and higher locomotory efficiency have a common cause, where both speed and efficiency depend on frontal area which may partly drive form and pressure drag forces. However, this hypothesis is not supported by the distribution of COT across architectures (Fig 6C, D), where except for the less-efficient oblique chains, all architectures present similarly efficient COT values. Perhaps there are other underlying explanatory factors linking swimming speed and swimming efficiency, such as shared ancestry, muscle content, jet coordination, or jetting angles (thrust-to-torque ratios).

*Evolutionary implications*

Across the evolutionary history of salps, linear chains have evolved multiple times independently from oblique ancestors (Damian-Serrano et al. 2023), suggesting the adaptive role of this architecture as a functional trait. Linear chain architectures evolved independently in *M. hexagona, S. zonaria, I. punctata*, and before the common ancestor of *Iasis* and *Salpa*. Our results show that going from an oblique form to a linear one may confer significant advantages in locomotory speed and energetic efficiency. However, multiple colonial architectures, which we find to be slower swimmers (such as transversal chains, helical chains, whorls, and clusters in the genus *Pegea* and the Cyclosalpidae family) had also evolved from oblique and linear ancestors. This is incongruent with a scenario where natural selection strongly favors locomotion efficiency across all ecological niches of salps. Therefore, the evolution of colonial architecture may be driven by ecological trade-offs with other non-locomotory functions. Alternatively, in some of these lineages, locomotion at the colonial stage may not be important enough for selection to maintain these highly streamlined forms, allowing for neutral evolutionary processes to produce a diversity of non-adaptive forms.

In the current study, we did not use phylogenetic comparative methods in our analysis because like other investigators comparing biomechanical properties across species (e.g. Dabiri et al. 2010, DiSanto et al. 2021) we were interested in inherent mechanical relationships dictated by the colony architectures. For instance, a linear arrangement of zooids inherently reduces drag due to a cluster arrangement, leading to faster swimming speeds and potentially higher efficiency regardless of phylogenetic history (Taylor & Thomas 2014). In other words, any phylogenetic inertia is irrelevant in instantaneous relationships between traits (Felsenstein 1985). Moreover, independence of data is often incorrectly assumed to be an assumption of standard (nonphylogenetic) regressions (Uyeda et al. 2018), when in reality the assumptions relate to the independence and distribution of the error terms. Though Uyeda et al. (2018) focuses on singular-event evolution, which is not the nature of the present study, the statement is broadly relevant to comparative regressions. Thus, when all the phylogenetic signal is present in the predictor, as it is in the case with colonial architecture (Damian-Serrano et al. 2022) and its associated characteristics, there is no need for a “phylogenetic correction” (Uyeda et al. 2018). However, there may be unaccounted factors explaining the residual variation in our analyses that bear phylogenetic signal (Autumn et al. 2002). For example, tunic stiffness, tunic smoothness, muscle band number, muscle fiber density, swimming behavior, as well as metabolic and physiological baselines may be more similar between more closely related species, potentially erasing some of the architecture-specific signal. Future studies could address the role of phylogeny and heritable factors in salp swimming speed and cost of transport using phylogenetic comparative methods. These analyses could reveal whether these factors have co-evolved with each other and/or with respiration rate or colonial architecture.

*Insights for bioinspired underwater vehicle design*

Pulsatile jet propulsion is a promising avenue for bioinspired aquatic vehicles and robots (Mohensi 2006, Gohardini 2014, Yue et al. 2015). Multijet propulsion systems with multiple propellers akin to salp colonies have been explored in an engineering context (Chao et al. 2017, Costello et al. 2015) with direct inspiration from gelatinous animals (Marut 2014, Krummel 2019, Bi et al 2022, Du Clos et al. 2022). Salp diversity provides a natural laboratory to explore the hydrodynamic implications of different multijet arrangement designs. Our findings underscore the importance of considering the scaling hydrodynamic properties of propeller arrangements to optimize speed and energy efficiency in bioinspired underwater vehicle design. While linear chain arrangements were the fastest and among the most energy efficient, robot (or vehicle) configurations such as a cluster form may confer unique object manipulation or maneuverability advantages. Our results show that these seemingly inefficient propeller configurations do not impose large disadvantages in terms of speed and fuel efficiency.

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**Data availability**

Data used to generate the results presented in this paper are available in the supplementary information. Any other datasets used directly or indirectly for this study are available from the authors upon reasonable request.

**Competing interests**

No competing interests declared.

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