

EFFECTS OF FLOW VELOCITY AND SETTLEMENT LOCATION ON GROWTH RATES
OF EARLY JUVENILES OF THE PEDUNCULATE BARNACLE, *POLLICIPES*
POLYMERUS, SOWERBY 1833

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Abstract

The intertidal lepadomorph barnacle, *Pollicipes polymerus*, is known for its propensity to aggregate in rosette-shaped or irregular clusters. The gregarious lifestyle is ensured by the species' settlement preference. Cyprids of *P. polymerus* settle almost exclusively on the peduncle of adult conspecifics, while settlement in cracks and crevices and on acorn barnacles is rare. For gregarious settlement behavior to evolve and persist, individuals should gain some benefit that would otherwise not be achieved with a solitary lifestyle - such as defense against predators (Riipi et al. 2001) or to facilitate cross-fertilization (Wu 1981) Due to increasing demand for *P. polymerus* in culinary markets, the gregarious settlement behavior makes them particularly susceptible to overharvesting. This study examines whether gregarious settlement results in higher growth rates of juveniles compared to growth of solitary individuals. I asked if and how *P. polymerus* gains in overall fitness from gregarious settlement. I address two questions: 1) Is the growth rate of early juveniles dependent on the velocity of water in which they feed? and 2) Does settlement on conspecifics benefit early juveniles by increasing growth rate? Two treatment groups (solitary and gregarious) were studied, with individuals ranging in size from 1mm - 3mm rostro-carinal length. An apparatus, utilizing a rotating disc, was constructed to create a range of experimental velocities. For two trials carried out in a marina environment (trial 1 and 2), growth rates ranged from 0.1mm - 1.2mm/wk at any given velocity. For two trials in a tank environment (trials 3 and 4) individual growth never exceeded 0.6mm/wk. Overall results indicate that neither current velocity nor settlement location had consistent effects on early juvenile growth rates. In the tank environment, where food concentrations were lower, velocity had a significant negative effect on the growth rate of gregarious but not solitary juveniles. In only 1 of 4 trials, settlement on a conspecific had a significant positive effect on average juvenile growth. The absence of consistent trends within and across trials together with few significant results indicate that velocity and settlement location for early juveniles may not be primary factors in gregarious settlement of this barnacle. Other factors or these factors at different life stages may account for settlement behavior. My findings also suggest that aquaculture of these barnacles does not require specific flow speeds or adult substrata to cultivate newly settled barnacles.

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Introduction

Anyone who has wandered the rocky intertidal of the Oregon coast surely will have noticed a creature who, along with others of its species, aggregates in irregular to rosette-shaped clusters attached to the underlying rock substrata. This unmistakable species, known as the gooseneck barnacle, *Pollicipes polymerus* has a range along the coast of the Northeastern Pacific from Susk, British Columbia to Baja California Sur (Pilsbry 1907, Cimberg 1981). Their intertidal occurrence overlaps primarily with that of the bivalve *Mytilus californianus*, the upper range of their seastar predator, *Pisaster ochraceus*, and the lower range of acorn barnacles *Chthamalus* sp. and *Balanus glandula* (Barnes and Reese 1960). European gooseneck barnacles (*P. pollicipes*) are regarded as a culinary delicacy, particularly in Spain and commonly known as percebes. The meat of fresh *Pollicipes* can command as much as eighty USD per kilogram and the price only continues to climb (López et al. 2010, Gardiner 2015). Being of high economic value (Bingham et al. 2017, Romersa 2018), gooseneck barnacle populations are subject to overharvesting. This poses a significant threat to the population's ability to restore itself for the unique reason that *Pollicipes* cyprids almost exclusively settle on the peduncle of conspecifics.

Although rare, *P. polymerus* has been known to settle in small cracks and crevices that resemble, at the microscopic scale, the interscalar spaces in which they typically settle on a conspecific's peduncle. (Barnes and Reese 1960) Aggregative or gregarious settlement behavior is seen across a plethora of species though the mechanisms by which it is achieved and the ecological benefits behind it vary by species. For gregarious settlement behavior to evolve, natural selection should provide some benefit that would otherwise not be achieved with a solitary lifestyle - such as defense against predators (Riipi et al. 2001) or to promote cross-fertilization (Wu 1981).

For *Pollicipes polymerus*, no scientifically supported benefit is known for early juveniles who's larval cyprid settles on larger conspecifics. The resulting rosette-shaped clumps are an apparent outcome of their gregarious settlement, but the answer as to what these clumps offer an individual or population remains elusive. Potential benefits notwithstanding, research has shown that the species possess certain mechanisms which ensure that gregarious settlement perpetuates. Lewis (1975) found lab reared larvae of *P. polymerus* could only be stimulated to settle in the presence of a healthy, adult conspecific. Hoffman (1988) pondered the cirripede's ability to settle on peduncle-like substrate after observing *P. polymerus* juveniles on a settlement plate only after acorn barnacle spat accumulated on the plate. Helms (2004) studied the precise placement of *P. polymerus* spat around an adult's peduncle and proposed a mechanism of capitular hydrodynamics which traps conspecific larvae in an eddy directing it toward the adult's capitular-peduncle junction.

Still questions remain: Do these clusters prevent desiccation, discourage predation, and/or create more favorable micro-environments in which juveniles can thrive? Furthermore, do the potential advantages of gregarious settlement change from one life stage to the next? Finally, can the realized benefits, whatever they may be, even be quantified? Ultimately, we need to know whether the overall fitness of individual *P. polymerus* improves due to gregarious settlement. Individuals are highly vulnerable in the early stages of life and thus their need for mediation of the environment may be at its highest during this period of development.

This study examines growth rate of juveniles to determine if any benefit results from gregarious settlement. I address two questions: 1) Is the growth rate of early juveniles dependent on the velocity of water in which they feed? and 2) Does settlement on conspecifics benefit early juveniles by increasing juvenile growth rate? The hypotheses are that 1) growth rates of early juveniles will be slower at the lowest experimental velocities and 2) growth rates of early juveniles will be greater for individuals settled on adult conspecifics.

Materials and Methods

Specimen collection

Specimens were collected from wave exposed rocks in the intertidal zone near the entrance to Coos Bay estuary (43°21'00.3"N 124°19'54.2"W). Collection occurred between May and July of 2021. Boulders on which the *P. polymerus* clusters reside, and *P. polymerus* clusters themselves were chosen at random. Clusters surrounded by or next to mussel beds (*Mytilus* spp.) were excluded. A crowbar and hammer were then used to separate clusters including some of the rock surface from the boulders to avoid rupturing or otherwise compromising the peduncles of adult *P. polymerus*. Harvested specimens came from the edge of clusters, and no more than one third of a cluster was removed at any one time. Collected organisms were placed in a sea table at 11°C, with air stones and constant supply of unfiltered seawater, for four days to confirm survivorship.

Experimental velocity gradient

To create a velocity gradient in which to place the barnacles, I built an apparatus consisting of a 60 cm diameter plexiglass disc connected at its center by an axle and bearings to a variable speed motor. The apparatus was oriented so that the disc was horizontal below the surface of the sea water with the shaft extending up out of the water to the motor. (Figure 1a)

Four plexiglass strips (27 cm x 2.5 cm x 0.5 cm) were attached to the underside of the plexiglass disc as four equidistant spokes. (Figure 1b) Two of the strips, located opposite each other, had inverted 1.5mL microcentrifuge tubes attached by superglue to the strip at 2 cm intervals. Individual juvenile *P. polymerus* were attached by superglue at the widest part of the conical end of the microcentrifuge tube. Individuals on these strips were part of Treatment 1 and are referred to throughout the study as solitary juveniles. The other two strips had *P. polymerus* adults attached 2 cm apart with superglue directly to the plexiglass strip. Juveniles on the peduncle of adults on these plexiglass strips were part of Treatment 2 and are referred to as gregarious juveniles. All organisms were attached to their substrata in the same orientation ensuring their extended cirral fan would face oncoming water. Barnes and Reese (1960) described the species as consistently achieving capitular orientation that faces the rush of water subsequent to a wave breaking. While the organism can achieve the preferred orientation itself, the time scale and data necessary for this project required that optimal capitular orientation for feeding be established at the start of the experiment. During a trial, organisms were fully submerged for 24 hours per day, every day of the trial. Trials lasted between two and three weeks.

To calculate the free-stream flow velocity (v) experienced by a *P. polymerus* juvenile at any given distance from the disc center (r) each juvenile's distance along the disc radius was recorded as well as the time elapsed for one complete rotation of the disc (t). Velocity was thus calculated using the following equation:

$$v = \frac{2\pi r}{t}$$

The experimental free-stream velocities ranged from +15 cm/s to +180 cm/s. The upper end of the velocity gradient was limited by equipment available. The local velocities experienced at the level of the cirral fans were less than the free-stream velocities due to the presence of the boundary layer and possible entrainment of water by the rotating disc, but local velocities were not measured.

Four trials examining growth of juveniles

Trials 1 and 2 were performed in the field at the Charleston Marina in Charleston, OR (43°20'44.0"N 124°19'41.7"W). Motor and shaft were secured to a floating dock. The plexiglass disc rested horizontally in the water column 20 cm below the surface of the water. At the lowest low tide of the season, the disc was positioned 0.5 m above the ocean floor. A 1 m radius oil-sorb semicircle attached to the dock on either side of the disc prevented the collection of flotsam drawn in by the vortex from the spinning disc.

Due to concern of marina pollutants potentially affecting the growth of the study organisms, trials 3 and 4 were performed in a rectangular tank (1.7 m x 1 m x 0.4 m) at the Oregon Institute of Marine Biology campus. The horizontal disc was situated in the center of the tank, 15 cm below the surface of the water and 15 cm above the tank bottom. Fresh filtered seawater at 10°C was continually pumped into the tank. The contents of a 20-minute plankton tow with a 130µm net were added to the tank as a food source on a daily basis. The tow was performed at the outer end of F-dock of the Charleston Marina one hour prior to high tide.

Growth rate

Three days prior to commencement of a trial, the initial rostro-carinal length (RC_i) of each juvenile was recorded to the nearest 0.1 µm using the calibrated reticle on a dissecting microscope. The size of experimental individuals ranged from 1mm-3mm RC. Treatment 1 juveniles (solitary) were removed from adult peduncles by dissecting forceps. Once measured, juveniles were attached with superglue to the inverted microcentrifuge tubes and floated in a sea table for three days to confirm survivorship. Treatment 2 juveniles (gregarious) were located along the stalk of adult conspecifics. Non-target juveniles were preened from the adult's peduncle so that the number of target juveniles on a stalk never exceeded two. Upon completion of a trial, the barnacles were preserved in 70% EtOH and stored in the dark at room temperature. Mortality was documented and considered as absence of the individual or RC_f lengths that were equal to or less than the individual's initial RC. Final rostro-carinal measurements (RC_f) were recorded within five days of trial completion. Growth rates (GR) in this study are quantified as millimeters of RC growth per week determined as:

$$GR = \frac{RC_f - RC_i}{\# \text{ of weeks in trial}}$$

Data Analysis

For treatments 1 and 2 (solitary and gregarious), growth rates of juvenile *P. polymerus* from each of the four trials were graphed as a function of flow velocity on separate scatter plots. Correlation coefficients and two-tailed p-values were calculated for each scenario (Zar, 1984). Data was not transformed to take into account differences in RC_i lengths because juveniles on either end of the size spectrum exhibited some of both the highest and lowest observed growth rates.

Because the water velocity only impacted growth of one treatment in each of only 2 trials, growth data for each trial were analyzed with a t-test comparing treatments (*solitary versus gregarious*) using JMP statistical software.

Results

Effect of velocity on growth rate

Growth (change in RC/week) was highly variable in both treatments for all four trials. While mortality occurred (36% for solitary treatment; 39% gregarious treatment), it was not obviously related to a particular velocity or range of velocities. In addition, because overall mortality was higher for gregarious juveniles, it was concluded that mortality data for solitary individuals was not a result of the transplant process. For both treatments, there was either no effect of velocity on RC growth, or a negative effect at higher velocities for one of the two treatments in a trial. In trials 1 and 2, growth rates ranged from 0.1mm/week to 1.0mm/week, while in trials 3 and 4, growth rates ranged from 0.1mm/week to 0.6mm/week. In trials 1 and 2 (Charleston marina) there was no significant effect of velocity on growth for either of the two treatments. Growth rates in treatment 1 of trial 2 had the lowest correlation to velocity compared to all other trials (Table 1 and Figure 2).

In trials 3 and 4 (rectangular tank) growth rate of individuals in treatment 1 did not vary with flow velocity. However, individuals in treatment 2 had significantly slower growth rates at higher flow velocities in both trials (Table 1, Figure 2).

In all other models, positive and negative correlations were nonsignificant between growth and velocity (Table 1). Overall, this suggests growth rate in *P. polymerus* juveniles was not impacted by the velocity of water in which they feed.

Effect of settlement location on growth rate

Because of the limited effect of flow velocity on juvenile growth rate, the data for each treatment were treated as population samples and the mean growth rates were compared between treatments within trials. For three of the four trials (1, 3, and 4), there was no significant difference in growth rate between the two treatments (Table 2). The only statistically significant difference in growth as a function of settlement location occurred in trial 2 (marina environment) in which juveniles in treatment 2 demonstrated greater growth rates than those in treatment 1. *Pollicipes* juveniles grew at a given rate regardless of whether they settled on primary substrate or the peduncle of a conspecific. (Table 2).

Discussion

Effect of flow velocity on early juvenile growth rate

The results of this study show that continuously submerged juveniles of *P. polymerus* grew at a rate that was independent of the flow velocity of water in their immediate environment. The temperature and nutritional conditions during the study were similar to the natural environment, with water temperatures around 9°C (NERRS 2021) and a range of flow velocities between +15cm/s and +180cm/s. The growth rates observed in this analysis (0.1mm/week to 1.2mm/week) were greater than those reported in other studies of juvenile *P. polymerus* in similar environmental conditions: 0.2mm - 1.2mm RC growth per month (Jacinto et al. 2015, Lewis and Chia 1981, Paine 1974). Hoffman (1988a, 1988b) reported juvenile growth rates between 4mm and 9mm per month in warmer coastal waters around 20°C of southern California.

Page (1986) found that the average capitulum height growth rate of permanently submerged adult *P. polymerus* on offshore oil platforms was 3.5 times that of coastal individuals subject to tidal fluctuations. The specimens in this study were fully submerged for the entirety of their trial. Although no literature exists corroborating the relationship of *P. polymerus* capitulum height (length from base of capitulum to top of tergum) growth with RC growth, it stands to reason that there is a positive correlation between the two. Based on this assumption, one could deduce that RC growth rates increase from cold temperature, tide influenced populations to maximum growth rates in warm temperature waters with permanent submerged environments.

It is also possible that water quality in the marina environment in trials 1 and 2 negatively impacted RC growth in comparison to what could be achieved in a natural environment. Even so, this study's growth rates were higher than intertidal juvenile rates reported by Paine (1974) and Lewis and Chia (1981) thus supporting the use of the Charleston marina as a viable substitute for in situ water parameters.

In a tank environment, average growth rate for both treatments was half that for individuals in the marina environment. The slower growth seen in individuals from the tank trials (3 and 4) is likely a result of insufficient amounts of food. While the amount of phytoplankton in the tank was high (judging by the color of the added plankton), *P. polymerus* juveniles', sized 1mm - 6mm RC, diets consist primarily (92%) of organic particulate matter with diameter less than 10µm (Lewis 1981). Not only are juvenile feeding appendages in this size class smaller than those of adult conspecifics, they employ an entirely different mode of feeding called pumping, often observed in acorn barnacles of all sizes (Lewis 1981). The frequency of pumping in *P. polymerus* juveniles decreases in faster currents, eventually ceasing altogether, and is replaced by continuous extension of the cirral fan, as seen in adult conspecifics. (Lewis 1981) However, Lewis did not specify what constituted a fast current, so the exact threshold at which pumping ceases is not known.

It is possible that Lewis' threshold was surpassed in this particular experiment since fast current in the Lewis study was described as being faster than "calm water of laboratory tanks". It is not clear at what velocity the juvenile's switch feeding behavior or whether feeding behavior changed along the experimental range of velocities. Trager et al. (1990) found acorn barnacle *Semibalanus balanoides* switched from active-pumping to passive cirral extension at 3.10cm/s. Furthermore, it is unclear if the switch in behavior is a response to greater concentrations of particulates passing the organism in a given amount of time, or perhaps faster currents preventing pumping behavior in some way. Interestingly, Barnes and Reese (1960) found that

stimulation of cirri by a water jet yielded a prompt capitular reorientation from *P. polymerus*, so it is likely the juveniles' cirri are receiving some form of input from the faster current and responding to it in kind.

Across an experimental velocity gradient of 15cm/s - 180cm/s in a tank environment, flow velocity seemingly had no effect on the growth rate of continuously submerged, solitary, juvenile *P. polymerus* (treatment 1). The growth rate of gregarious juveniles (treatment 2), however, appears to have been negatively affected by increased flow velocity. Taking into account the dominant particle size of available food (>130µm), it appears that growth rates of *gregarious* juveniles decrease as current velocity increases when appropriately sized food abundance is low. If we consider the immediate proximity of adult conspecifics, whose diet consists of particulate (<10µm, 52%) and large (>10µm, 40%) organic matter, it is possible that the adults negatively impact nearby juvenile growth, with the effects increasing in magnitude as current velocity increases.

Prior to data collection, I hypothesized that growth rates of early juveniles would be slower at lower current velocities. Average maximum speed of breaking waves for a wave-exposed rocky intertidal ranges from 4.26m - 4.41m/s (Marchinko 2003), so the higher end of the experimental velocity gradient was intended to mimic moderate flow velocities experienced in situ. The lower end of the gradient was meant to simulate flow velocities slower than what would typically be experienced in the natural environment. Eckmann and Duggins (1993) reported no change in growth rate of adult *P. polymerus* over a narrow velocity gradient (2cm - 14cm/s) and interpreted this as unsurprising as *P. polymerus* is known to inhabit exclusively high-energy environments. Additionally, the shelter provided by a conspecific cluster leads one to question the conditions and microenvironment present within a *P. polymerus* cluster - an environment in which current speeds are moderated by eddies, shear, and boundary layers. While my study did not examine the microenvironment surrounding solitary or gregarious juveniles specifically, it was designed to mimic and manipulate a potential circumstance within the cluster. Whether or not a microenvironment with moderated velocity exists remains to be seen. As a hypothetical facet of the microenvironment, however, moderated (a.k.a. slower) flow alone does not positively affect early juvenile growth rate to the degree that it is a driving force for evolution or maintenance of gregarious behavior.

Effect of settlement location on early juvenile growth rate

The effect of settlement location on early juvenile growth varied between trials. Only one of four trials was significant (Table 2) with faster growth occurring on conspecifics. However, growth rates of solitary or gregarious juveniles were not different in the other three trials. Unlike the relationship between flow velocity and growth rate found in the tank trials (Trials 3 and 4), this result occurred in the marina (trial 2).

Although the overall analysis did not demonstrate a relationship between growth rate and settlement location, the significant results from trial 2 question the veracity of that claim. For one, the substantially larger sample size of trial 2 not only gives some confidence to the probability value, but also calls into question the results of the other trials. In other words, trials 1, 3, and 4 may have been insufficiently powered to detect a true difference - suggesting a comparison of larger populations may have different results.

Another possible explanation for the observed results is that the duration of the trial was too short to see any significant trends in growth rate. Cirripeds are known for the phenotypic plasticity of their cirral fans and subsequent propensity to alter fans in response to the flow of their environment (Marchinko 2003b). The range in balanomorph plasticity is much greater than that of gooseneck barnacles due to acorn barnacles inhabiting a variety of environments subject to different degrees of wave-exposure. Even so, 92% of variation in *P. polymerus* leg length can be explained by water velocity (Marchinko 2003a). This plasticity is achieved by molting, a process that begins in *P. polymerus* adults to occur eight days following perturbation in experimental systems, with subsequent molts exceeding thirty days. (An et al. 1971, Page 1983) Given these temporal relationships with adjustments in cirral dimensions and the resultant increase in feeding efficiency for a given flow environment, trials in this study would have had to last for at least thirty days or longer to see if the effects translate to increased growth rates, assuming *P. polymerus* juveniles molt at the same rate as adults. If my trials (two- and three-week durations) had lasted longer, the juveniles may have adjusted cirral fan dimensions in accordance with the conditions of their settlement location and flow velocity, and greater growth rates may have been observed. Waters with in situ nutritional concentrations would be crucial because Page (1983) found that ration alone can influence molting frequency between thirty-one and forty days.

Finally, it is unlikely that the gregarious treatment adequately simulated naturally occurring conditions in a cluster of *P. polymerus*. It would be difficult to recreate the conditions of the inside of a cluster and maintain the experimental design measuring the original variables (RC growth with respect to flow velocity). The method behind this particular study, however, was to mimic conditions at the edge of a cluster. Helms (2004) found that juveniles grew faster when settled on adults at the edge of a cluster than did juveniles on adults in the center of clusters. Ideally, effects would be more immediately discernible by attempting to achieve “edge conditions”. Because this study did not examine growth rates of juveniles surrounded by more than one conspecific, it is difficult to say whether or not the faster growth rates associated with “edge conditions” were present. It also begs the question: Does having fewer adult conspecifics in the immediate vicinity result in faster growth? Or is there a limit to the minimum number of proximal conspecifics at which point any further decrease would mean slower juvenile growth? If this were true, we may expect to see higher growth rates on solitary juveniles, but that did not occur. Further examination of this hypothesis, such as a treatment where juveniles are at primary substrate level rather than up on a promontory (which would more closely simulate conditions of the cyprid settling on rock substrata) may help us to understand the costs and benefits of gregarious settlement at the early juvenile life stage.

The second hypothesis of this study was that the growth rate of early juvenile *P. polymerus* would be greater for individuals settled on adult conspecifics. It was postulated that gregarious settlement would be preferred to solitary settlement in early life stages because the benefit of immediate proximity to an adult conspecific would increase fitness by increasing a juvenile’s growth rate. However, the results of this study suggest that neither attachment nor proximity to an adult conspecific improves early juvenile fitness to the effect that it boosts growth beyond what is seen in solitary juveniles.

Conclusion

A gregarious lifestyle common among some biota is thought to increase an individual's overall fitness and thus the likelihood that they successfully reproduce. In this study, growth rate was used as a measure to quantify increased or decreased fitness of early juveniles of *P. polymerus*. Both flow velocity and settlement location were manipulated to assess the dependence of growth rate on either factor. The experimental velocity gradient, containing both natural and unnatural water speeds, proved inconsequential to growth rate for juveniles in a marina environment. In an environment with limited nutritional resources, increased velocity negatively affected gregarious juvenile growth while growth of solitary juveniles remained independent of flow velocity. Excluding velocity as a contributing factor, a comparison of average growth between solitary and gregarious treatments proved significant in only one of the four trials. Across all trials, the analysis suggests that settlement on a conspecific does not improve growth rate and therefore fitness of juveniles. Improved growth rate, at early *P. polymerus* life stages, may not be a direct benefit of gregarious settlement.

Tables and Figures

Table 1 – Results from linear regression for trials and each treatment comparing effect of flow velocity on juvenile rostro-carinal growth rate. Trial 1 and trial 2 (marina environment), trial 3 and trial 4 (tank environment), treatment 1 (solitary juvenile), and treatment 2 (gregarious juvenile). * represents a significant result.

Trial	Treatment	R²	r	n	df	p-value
1	1	0.075	0.274	22	20	<0.50
1	2	0.008	0.0894	20	18	>0.50
2	1	0	0	30	28	>0.50
2	2	0.003	0.0548	35	33	>0.50
3	1	0.015	0.122	21	19	>0.50
3	2	0.262	0.512	32	30	<0.01*
4	1	0.062	0.249	26	24	<0.50
4	2	0.156	0.394	31	29	<0.05*

Table 2 – Results from two-tailed t-Tests on RC growth (mm/wk) by treatment for each trial. Trial 1 and trial 2 (marina environment), trial 3 and trial 4 (tank environment). * represents a significant result.

Trial	df	t-ratio	Prob > t
1	40	-0.0005	0.9996
2	65	3.848	*0.0003
3	53	-0.0755	0.9402
4	55	1.534	0.1308

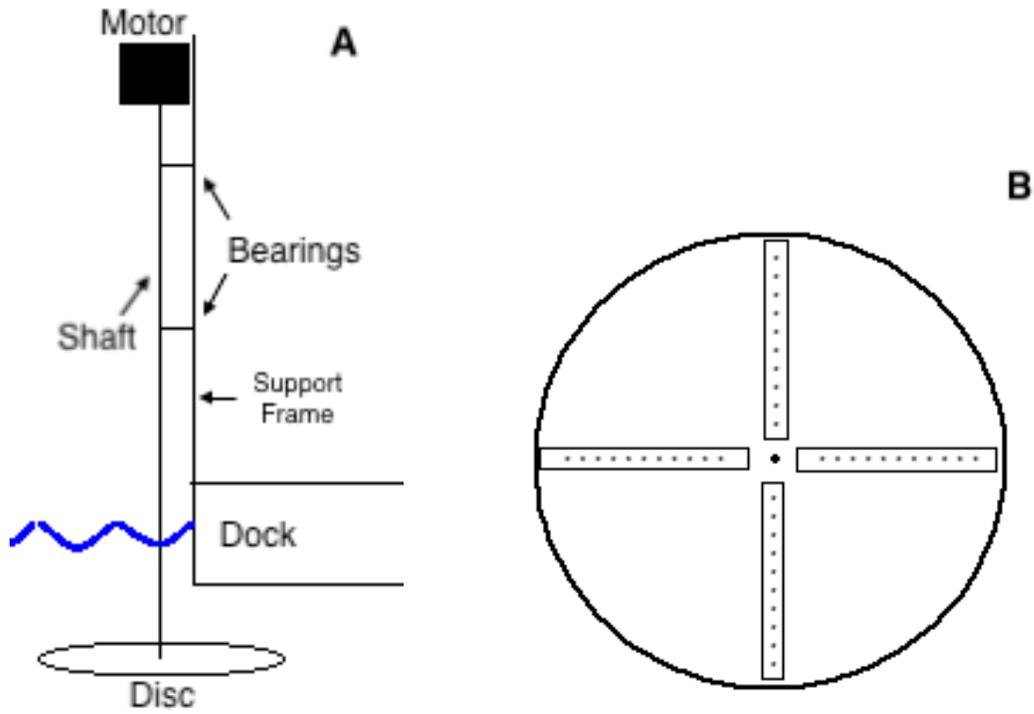


Fig. 1 - (A) Side-view schematic of spinning disc apparatus. Setup is depicted in the Charleston Marina environment. (B) Underside view of plexiglass disc and the four attached plexiglass strips to which the barnacles were adhered.

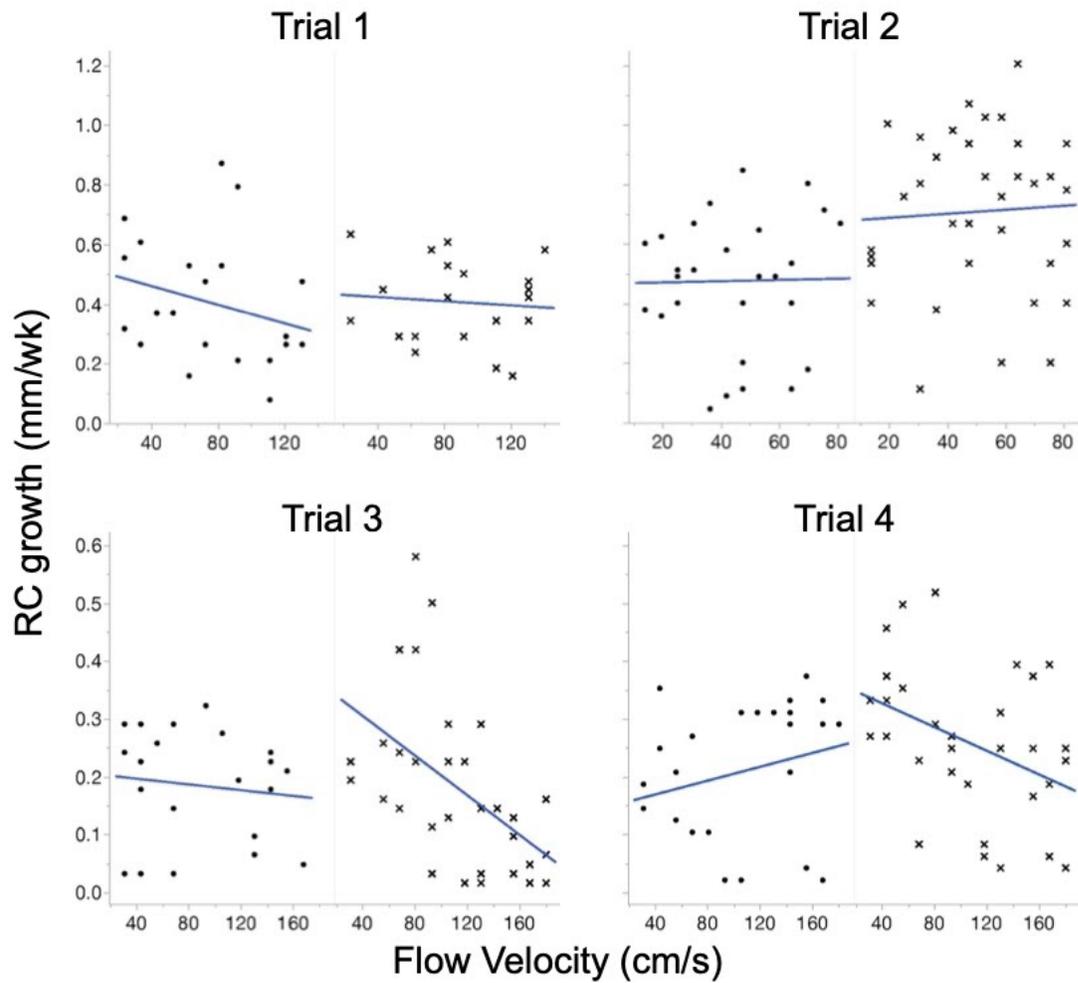


Fig. 2 – Scatter plots for all four trials. Blue Line models linear regression. Treatments in like trials are shown on the same graph side-by-side; treatment 1 left panel (•); treatment 2 right panel (×).

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